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Anatomy and Functional Morphology of Dermal Collagen Fibers in Sharks

P. J. Motta

The dermis of sharks consists in part of a highly ordered array of collagen fibers. These fibers form layers of alternately oriented sheets that run in helical paths around the shark's body. The fibers of one layer are directed from dorsocranial to ventrocaudal, and the fibers of the other from ventrocranial to dorsocaudal.

The angle that the collagen fibers make to the longitudinal axis of the shark vary from 90° in the occipital region to almost 0° in the caudal fin, the majority of the angles lying between 50° and 70°. Fibers lying within the latter range are believed to undergo no change of length during swimming, therefore imposing no restriction on the swimming shark.

The numerous layers of these strong collagen fibers, closely bound together by cross-over collagen fibrils joining the different layers, is believed to serve at least in part a mechanically protective function and possibly as a firm anchorage for the body musculature.

Single layers of the more superficial collagen fibers overlie the ceratotrichia of the caudal fin lending support to the flexible ceratotrichia and probably giving the fins additional support and rigidity.

DERMAL collagen fibers have been described in teleosts: The flathead sole, *Hippoglossoides elassodon* (Brown and Wellings, 1970), the goby, *Chasmichthys gulosus* (Fujii, 1968) and the mummichog, *Fundulus heteroclitus* (Nadol, 1966; Nadol, Gibbins and Porter, 1969 and Jackson, 1968). The function of these fibers in the tail of *Sarotherodon* (=*Tilapia*) *nilotica* has been investigated by Videler (1975), and in the tail of the sturgeon *Acipenser ruthenus* by Smith (1956). Johnels (1950) described the fiber development in the lamprey, *Petromyzon fluviatilis* and commented upon its probable evolutionary history.

The number and nomenclature of the elasmobranch layers appear to be in much confusion. Andrew (1959) describes two layers in the dermis, a loose cellular outer one, and a compact inner one which lies upon the subcutaneous layer. He describes the subcutaneous layer as being composed of coarse compact bundles of collagen fibers. Jollie (1962) describes three layers in the dermis; an outer layer around the necks of the scales, the stratum laxum a laminated fibrous layer to which the scales are bound, and a deeper stratum compactum composed of horizontal and vertical fibers. He also notes a subcutaneous layer of variable thickness composed of a reticulum of fine fibers. Stockard (1944) describes the dermis as consisting of a stratum vasculare nearest the epidermis, and a deeper stratum compactum. The s. compactum is described as having compact, cross-lacing, connective tissue fibers.

A similar study of dermal collagen fibers of the teleost *Fundulus heteroclitus* has been conducted by Nadol, Gibbins and Porter (1969). They discuss the development and anatomy of such a fiber system, some aspects of which I have found to be duplicated in sharks. They describe a "scindulene (shingle)" theory for the basement lamella containing the highly ordered array of collagen fibrils. The lamella has 8 to 10 orthogonally arrayed layers of collagen fibrils. Collagen fibril layers in the dermis were observed to descend at a slight angle from their insertion points in the basement' membrane, similar to shingles on a roof. The fibrils are polymerized in one direction only in any given area of the basement membrane. These adjacent areas are oriented at 105°–110° to each other. Between the fifth and twelfth days after fertilization, 8–10 layers of these orthogonally arrayed fibers develop in the skin of *Fundulus heteroclitus.* They found that thickening of the lamella with growth until post hatching stages is the result of an increase in the number of rows of fibrils per layer, not in the number of layers.

Smith (1956) describes the dermis in the tail of *Acipenser ruthenus* as having approximately twenty-five strata of dense collagen fibers arranged in alternating diagonal layers, the fibers lying at an angle of 57° to each other. The scales of the tail are supported by about half of these fiber layers, so that the bases of the scales project into and are fused to about thirteen of the deeper fiber layers. The more superficial layers are stratified except where they approach a scale. Upon approaching the scale the more superficial fibers turn toward the scale and converge on its center. He also noted the presence of fibers running obliquely up into the scales from the deeper fiber region. Thus as he put it, the scale is a focus for fibers from all directions except externally.

Videler (1975) noted that the collagenous dermal fibers of *Sarotherodon nilotica* form layers of fibers running in two predominant directions lying at an angle of 47° to the body axis in the tail region. He noted a firm connection of the fibers to the heads and necks of the fin rays and to the shaft of the most dorsal and ventral fin rays. More peripherally to these tendinous connections he found that the raylets were covered only with a lining of stout connective tissue without the firm tendon connections.

MATERIALS AND METHODS

The dermal collagen fibers of *Rhizoprionodon terraenovae* (Atlantic sharpnose shark), *Ginglymostoma cirratum* (nurse shark), *Sphyrna lewini* (scalloped hammerhead) and *Mustelus canis* (smooth dogfish) were examined, fiber layers counted, and angle measuremens made on all except *G. cirratum*. Observations on the fibers were made on live *M. canis*.

Sphyrna were caught off the coast of Jamaica and off the North Carolina coast. Fiber angle measurements to the longitudinal axis were taken from a 60.5 cm female specimen from North Carolina. *Rhizoprionodon* specimens were caught in shallow water off the coast of Jamaica, observations were made on embryonic to mature specimens, and measurements made on a mature female. Mature *Mustelus* specimens were caught off the North Carolina coast and examined, and measurements made on a 44 cm male. *Ginglymostoma* specimens were caught in Jamaica and examined, they ranged in size from 74 cm to 183 cm.

All sharks caught off Jamaica were transported in 7.5% Formaldehyde and stored in 70% ethanol. Angle measurements were made only on freshly caught sharks. Sections of *Ginglymostoma* skin were both air dried and critical point dried using the Sorvall Critical Point Drying System, and then examined under a JEOL JSM-S1 scanning electron microscope.

TABLE 1. LOCATION AND METHOD OF SHARK ANGLE MEASUREMENTS.

Points A to O lie on longitudinal axis described below. Shark lying on right side, placed in swimming position.

A.	Above anterior origin of pectoral fin
B.	Posterior fused edge of pectoral fin
C.	Posterior free edge of pectoral
D. E. F.	Divide distance from posterior free edge of pectoral to anterior origin of pelvic by 4
G.	So G is anterior origin of pelvic fin
H.	Midway between anterior origin of pelvic and posterior fixed base of pelvic
I.	Posterior free edge of pelvic
J.	Anterior origin of anal fin
K.	Midway between anterior origin of anal and posterior fixed base of anal
L.	Posterior fixed base of second dorsal
M.	Midway between fixed posterior base of anal and lower caudal peduncle
N.	Upper caudal peduncle
O.	Midway between lower caudal peduncle and posterior intersection of upper and lower lobes of caudal fin
LONGITUDINAL AXIS:	Traces lateral line, then the tail is put in a position it would be if the fish were swimming and the line continues straight into the tail. Each of the above locations is divided into four angles to the above longitudinal axis. Each angle lies in one quadrant. The quadrants proceed clockwise, number one being the upper right quadrant. The result is that for each of the above locations (A to O), measurements such as A1, A2, A3, A4; B1, B2, . . . etc., are obtained.

Angle measurements were made at arbitrary

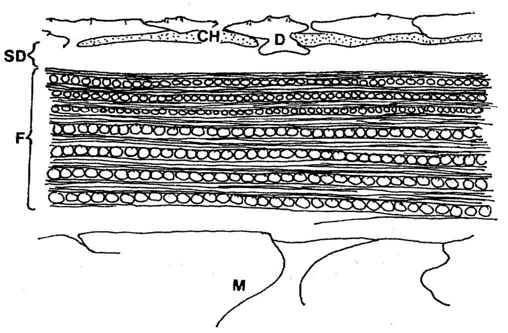

Fig. 1. Transverse section of *Rhizoprionodon terraenovae* skin taken slightly anterior and ventral to origin of 1st dorsal fin. F = stratum compactum; SD = superficial dermal region; D = base of denticle protruding into dermis; CH = chromatophores in uppermost part of SD; M = muscle tissue.

but consistent chosen points along the longitudinal axis of the fish. Table 1 describes these various locations. Estimated error in measuring the angles is ±2°.

Paraffin embedding was used to make 6 μm thick sections of the junction region between the fibers and the ceratotrichia in the caudal fin. These were stained with Mallory's stain. Sections 6 μm thick were also made using glycol methacrylate embedding, which were similarly stained.

Results

Fiber layering.—The dermal fibers under study are assumed to be collagenous. Andrew (1959) describes the coarse bundles of collagenous fibers found in the elasmobranch dermis, Moss (1972) also describes these as deep compact collagenous bundles. The fibers stained blue with Mallory's stain, adding support to their being collagenous.

In all sharks examined the dermis appears to be composed of two major regions. A more superficial region into which the bases of the denticles protrude, at which surface are found chromatophores nearest to the epidermis, and a deeper much wider region of alternately oriented layers of collagen fibers. At one point in the deeper region the fiber layers rapidly change in thickness (Fig. 1). The more superficial layers are thinner and it is impossible to tease apart individual fibers successfully, the deeper layers are thicker and individual fibers can easily be separated.

Apparently, what I describe as the more superficial dermal region, Jollie (1962) calls the stratum laxum and Stockard (1944) the stratum vasculare. What I describe as the deeper dermal region is called the stratum compactum by both of them, however Andrew (1959) notes a subcutaneous region of more tendinous and compact appearance, which seems to be the deeper thicker layers I described. I chose to call the region of alternately oriented collagen fiber layers the stratum compactum.

The fibers of the stratum compactum follow left and right hand helices around the body of the shark. Alternate layers follow different courses, either right handed or left handed helices. These fibers were exposed on a young *Rhizoprionodon* by carefully removing the epidermis. The fibers cover the shark from near the posterior end of the caudal fin to the anterior origin of the gill region. The fibers are most anterior dorsally in the occipital region and ventrally in the skin overlying the common coracoarcual muscle (Fig. 2). The gill region is covered only by the more superficial and thinner layers of the s. compactum. Removal of the epidermis in the occipital region exposes the anterior dorsal origin of the fibers originating at right angles to

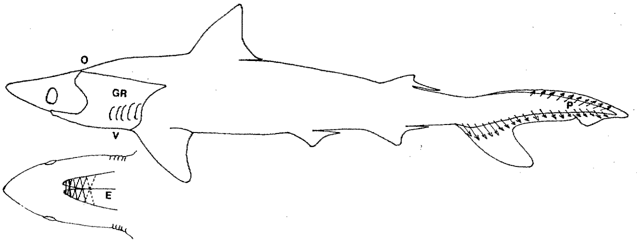

Fig. 2. Young female *Rhizoprionodon terraenovae*. O = occipital region; GR = gill region; V = anterior ventral origin of fibers; E = epaxial muscle bundle; P = posterior extent of fibers. Anterior dorsal origin of fibers and posterior extent of fibers explained in text.

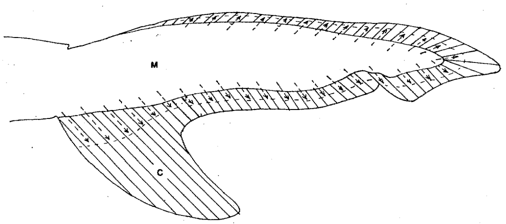

Fig. 3. Caudal fin of *Rhizoprionodon terraenovae.* Arrows indicate that a single layer of stratum compactum fibers overlies the ceratotrichia. C = cross-hatched area indicates ceratotrichia region; M = muscle tissue covered by alternately oriented fibers. Dotted lines indicate extent of fiber overlap on ceratotrichia.

the longitudinal axis of the fish lying above the anterior orgin of the epaxial muscle bundles. As the fibers proceed posteriorly they assume the acute angling to the longitudinal axis (Fig. 2).

The helical paths of these fibers are interrupted where they intercept the fins. Moss (1972) states that in the fins of all fishes only a basement membrane is present, the dermis being absent. The s. compactum fibers do overlie the caudal fin, and probably the other fins also. I can only speak with certainty concerning the caudal fin. Here the fibers continue over the muscle of the fin also covering the ceratotrichia and terminate short of the fin edge (Fig. 3). Sectioning and staining of the lower margin of the caudal fin in the region where the ceratotrichia begin reveals a single layer of the dermal fibers overlying and attached to the ceratotrichia only on the outer side of the latter (Fig. 4). Proceeding toward the edge of the fin the fibers become fewer in number and eventually terminate before the edge of the fin is reached (Fig. 5).

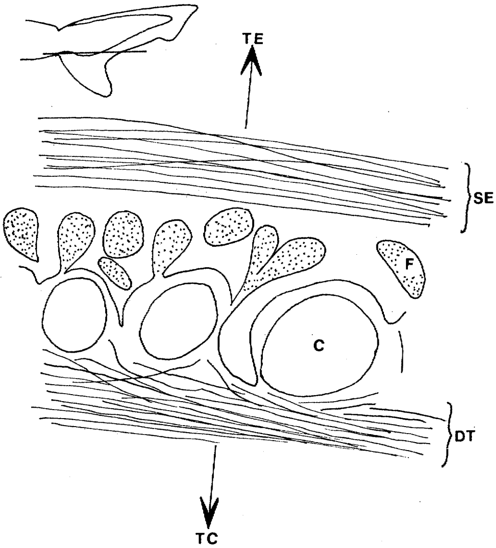

Fig. 4. Cross section through lower margin of caudal fin of *Rhizoprionodon terraenovae* showing stratum compactum fibers overlying and attached to ceratotrichia. SE = sub-epidermal layer; F = stratum compactum fibers; C = ceratotrichia; DT = dense tissue; TE = towards epidermis; TC = towards center of fin. Top left figure indicates region of cross section.

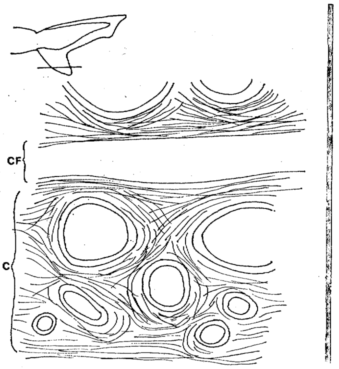

Fig. 5. Cross section through distal margin of the caudal fin of *Rhizoprionodon terraenovae* showing absence of stratum compactum fibers. CF = center of fin; C = ceratotrichia in loose connective tissue. Top left figure indicates region of cross section.

The dorsocranial to ventrocaudal fibers appear to all lie at the same angle to the longitudinal in a particular region, the same is true for the dorsocaudal to ventrocranial fibers. That is, at a particular region, the angle that an orientation of fibers makes with the longitudinal axis does not change amongst layers. Where the fibers cross the mid-dorsal ridge some of the deeper fibers fuse with the dorsal skeletogenous septum. Willemse (pers. comm.) states that the perimysial connective tissue fibers are continuous with a layer of connective tissue that A) interconnects the perimysial sheets and B) is attached throughout its surface to the compact layer of dermal connective tissue.

The number and thickness of stratum compactum layers was measured and reported (Table 2). Nadol et al. (1969) found that the adepithelial basement lamella in the skin of *Fundulus heteroclitus* had 8 to 10 layers of orthogonally arrayed collagen fibrils. These fibrils developed between the fifth and twelfth

TABLE 2. STRATUM COMPACTUM LAYERING IN FOUR SPECIES OF SHARK. Samples taken from dorsolateral region just anterior to caudal fin.

Shark	Length, sex, and stage of development	Total number of stratum compactum layers	Total thickness of stratum compactum layers	Number of deeper thicker s. compactum layers	Number of superficial s. compactum (thinner) layers	Total thickness of deeper layers	Total thickness of superficial layers
Sphyrna lewini	188 cm/♀ mature	22	1.6 mm	8–10	12	?	?
Sphyrna lewini	50 cm/♀ young	22	0.27 mm	10	12	?	?
Rhizoprionodon terraenovae	72 cm/♂ mature	14–15	0.63 mm	8	6–7	0.44 mm	0.19 mm
Rhizoprionodon terraenovae	37 cm/♂ embryonic	19–22	0.41 mm	8	11–14	0.23 mm	0.17 mm
Ginglymostoma cirratum	183 cm/♀ mature	43–46	3.88 mm	8–10	35–36	1.06 mm	2.81 mm
Ginglymostoma cirratum	73 cm/♀ young	43–46	1.28 mm	10–12	33–34	0.45 mm	0.83 mm
Mustelus canis	48 cm/♂ young	18	0.23 mm	?	?	?	?

days after fertilization, and subsequent thickening of the lamella with growth until post hatching stages was the result of an increase in the number of rows of fibrils per layer, not in the number of layers. Total thickness of the lamella in the adult fish was 3.6 μ, maximum collagen fibril diameter being 500Å. The number of layers of fibrils in the sharks varied (Table 2). Similar to *Fundulus*, thickening of the stratum compactum resulted from an increase in the number of fibrils per layer, not in the number of layers. Total thickness of the stratum compactum ranged from 3.88 mm in adult *Ginglymostoma* to 0.23 mm in young *Mustelus*.

Fine anatomy.—Jollie (1962) notes the presence of horizontal and vertical fibers in the stratum compactum. Nadol et al. (1969) notes that occasionally in *Fundulus heteroclitus* a fibril that stays with one layer will suddenly descend and merge with the next layer of fibrils having the same orientation, these they termed "crossover fibrils." They also note the presence of what they term "microfilaments" in the junction of the basement membrane and basement lamella, and throughout the lamella itself. Within the basement membrane they form a microgrid, the filaments crossing each other at approximately 95°.

As mentioned the deeper fiber layers of the s. compactum can easily be teased apart, one fiber at a time. In the more superficial thinner layers however this becomes impossible. In neither of these regions are the bundles of fibers free to slide. Crossover fibrils in the s. compactum were visible under the light microscope and S.E.M. pictures reveal these fibrils in greater detail. There is extensive crossing over between the layers. (Fig. 6.) The layers are securely linked by these crossover fibrils. The photographs are of the deeper region of the s. compactum, it is possible therefore that crossing over is more extensive in the superficial region and/or the crossover fibrils remain the same in number as those of the deeper region while the fibrils of the alternately oriented layers are fewer in number. Both of these methods would make removal of a single fiber in the superficial region more difficult than in the deeper region.

Observations on live sharks.—Live *Mustelus canis* were operated on, and an area of epidermis and more superficial dermis approximately 4 square cm was removed in the lateral region approximately midway between the first dorsal fin and the caudal fin. Undamaged deeper dermal fibers were exposed. Cutting the undamaged fibers in the recovered shark did not result in any observable change in length or

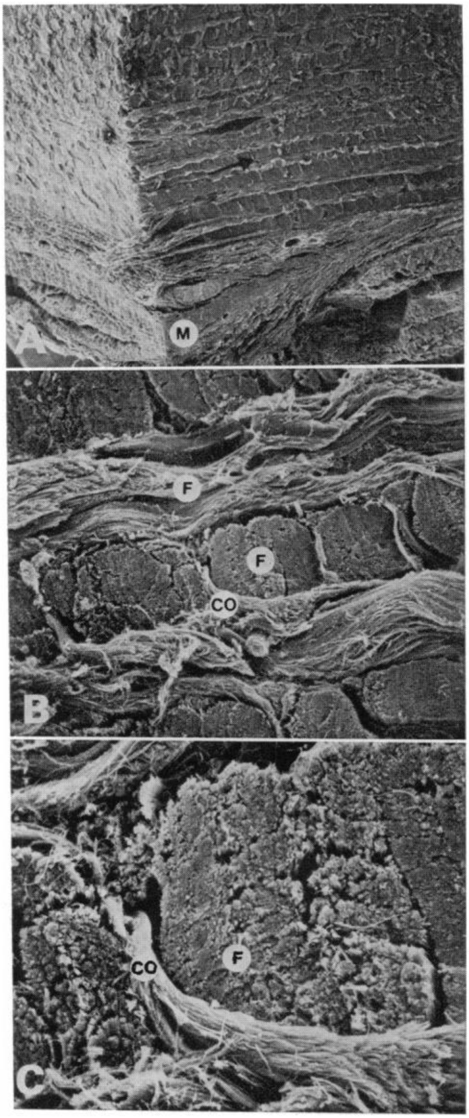

Fig. 6. Sections taken in orientation of one layer of stratum compactum fibers showing deeper dermal fiber layers of *Ginglymostoma cirratum*. Epidermis towards top of page. Magnifications of ×30, ×300, ×1,000. Arrow indicates region magnified. M = muscle tissue; CO = cross-over fibrils; F = stratum compactum fibers in alternate orientation.

pulling apart of the cut fiber ends. I assume that if there is any tension in the fibers it is extremely small. The fish was then bent forceably into a lateral flexure and the fibers cut again, there was no apparent pulling apart of the cut fiber ends on either the concave or convex side of the bend.

Observations on live *Mustelus* and *Ginglymostoma* show that upon lateral flexure during swimming, there appear regions of local buckling of the skin on the concave side of the belly, approximately between the origin of the pectoral fins and the pelvic fins.

Fiber angles.—Table 3 compares the fiber angles measured in four sharks. Figures 7–10 show the respective sharks with angles indicated. In nearly all cases, when a fiber crosses the horizontal skeletogenous septum its angle to the longitudinal axis changes. Within the particular sharks the angles in the third described quadrant (dorsocaudal to ventrocranial below the longitudinal axis) from positions A to I (anterior origin of the pectoral fin to posterior free edge of pelvic) are significantly greater than the angles in the remaining three quadrants from positions A to I, except in one case, that of the 60.5 cm *Sphyrna lewini* in the first quadrant (Mann-Whitney U-test, significant to 2.5%).

DISCUSSION

Connective tissue fibers in the dermis of all sharks examined that followed left and right handed helices around the body are assumed to be collagenous. This region of alternately oriented layers of fibers is termed the stratum compactum in keeping with Jollie (1962) and Stockard (1944).

There is a division in the layer thickness at one point in the stratum compactum. The more superficial layers being thinner, and the deeper layers thicker and generally less in number.

The intimate relationship between the dermal denticles and the s. compactum has not been investigated as has the relationship between the scales and fibers in the tail of the sturgeon (Smith, 1956). The denticles are however noted to be fused to the more superficial dermal region and unlike the sturgeon the great bulk of the dermis, at least in the trunk of the shark, lies much deeper to the base of the denticles.

The origin of fish scales from the dermal fiber system has been discussed by Jackson (1968) and its functional implications speculated upon by Breder (1947). Breder proposes that the scales of bony fishes limit the flexure on the concave side of the bending fish, the pattern, size, and distance between scales being important with regards to the degree of flexibility. This phenomena apparently is non-

TABLE 3. FIBER ANGLE MEASUREMENTS OF FOUR SHARKS (3 SPECIES). a = *S. lewini* 60.5 cm. b = *S. lewini* 188 cm. c = *R. terraenovae* 72 cm. d = *M. canis* 44 cm. Emphasized numbers indicate angles within a particular shark and location, that are significantly greater than angles in the other quadrants. The single exception is listed in the results.

	1				2				3				4			
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
	QUADRANTS															
LOCATION																
A	70	77	74	85	–	–	–	–	*64*	*75*	*80*	–	56	52	51	60
B	71	68	65	78	67	61	60	–	*66*	*73*	*75*	–	65	57	57	56
C	69	67	66	63	63	60	62	56	*69*	*77*	*71*	*67*	68	62	62	55
D	67	63	66	63	65	60	60	50	*69*	*77*	*71*	*69*	65	61	59	60
E	67	62	70	62	57	57	63	48	*71*	*75*	*71*	*72*	61	63	64	62
F	67	64	64	62	53	50	56	47	*74*	*73*	*71*	*70*	57	61	59	55
G	62	69	63	53	54	48	66	46	*67*	*70*	*68*	*62*	55	57	59	52
H	64	59	61	53	51	47	54	47	*66*	*70*	*68*	*62*	55	56	57	56
I	63	61	64	50	46	44	53	50	*66*	*72*	*66*	*63*	53	57	60	58
J	63	59	57	55	47	39	50	54	62	66	59	55	58	52	61	48
K	67	61	59	54	45	37	49	54	67	69	63	55	52	44	59	49
L	63	59	62	52	37	41	47	55	65	66	68	51	45	44	62	48
M	59	47	45	50	43	43	47	55	60	61	55	50	53	53	48	50
N	45*	31	47	40	39*	50	50	63	63*	45	47	40	49*	60	56	48
O	55*	32	45	–	56*	71	50	–	–	44	46	–	49*	68	60	–

* Large differences in locations N and O in sharks a and b may indicate caudal fins were not similarly placed in both sharks.

operable in sharks due to the small size of the denticles, and the probably more important function of hydrodynamics of denticle pattern is still uninvestigated.

Bonding of fiber layers to one another was observed in the deeper layers of *Ginglymostoma*. Similar bonding has been observed in both the superficial and deeper layers of the stratum compactum of an adult *Rhizoprionodon terraenovae*. What Nadol et al. (1969) describe as "crossover fibrils" appear to be very prevalent. Fibrils of one layer merge with both layers above and below it having the same orientation. Thus the fiber layers are bonded securely, preventing the sliding of layers over one another. Jollie (1962) may have been describing these crossover fibrils when he noted the presence of vertical fibers in the stratum compactum. At magnification up to × 1,000 these crossover fibrils appear to be the only manner of bonding between layers.

The number of layers in the stratum compactum vary among the species of shark examined. Increase in the thickness of the s. compactum is a result of the increase in the number of fibrils per layer, not in the number of layers. Comparing a 76 mm *Fundulus heteroclitus* with basement lamella thickness of 3.6 μ to the adult *Sphyrna, Rhizoprionodon* and *Ginglymostoma* studied, a relatively thicker stratum compactum occurs in these sharks as compared to the lamella thickness of *Fundulus.*

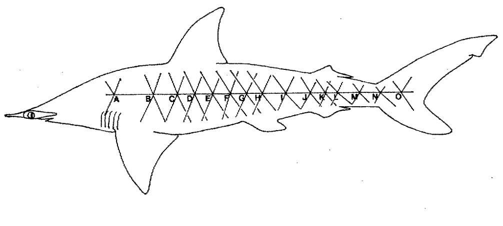

Fig. 7. *Sphyrna lewini* 60.5 cm, stratum compactum fiber angles to longitudinal axis indicated.

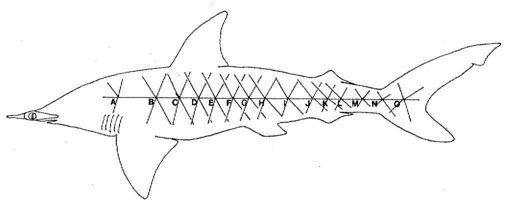

Fig. 8. *Sphyrna lewini* 188 cm, stratum compactum fiber angles to longitudinal axis indicated.

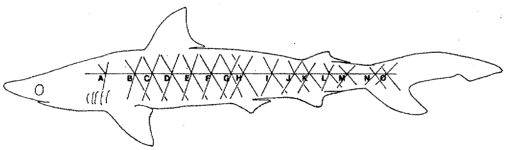

Fig. 9. *Rhizoprionodon terraenovae* 72 cm, stratum compactum fiber angles to longitudinal axis indicated.

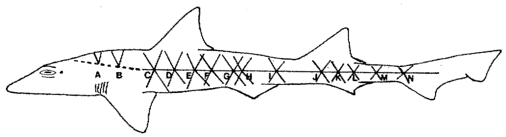

Fig. 10. *Mustelus canis* 44 cm, stratum compactum fiber angles to longitudinal axis indicated.

That is, if this 76 mm teleost was scaled up to the length of either a mature *Sphyrna* (188 cm) or *Rhizoprionodon* (72 cm) the s. compactum in the sharks would be 18 times thicker than the lamella in *Fundulus.* If the latter was proportional in length to *Ginglymostoma* (183 cm) the s. compactum of the shark would be 42 times thicker. The total thickness of the s. compactum in these sharks is, 1.6 mm, 0.63 mm, and 3.88 mm respectively.

At any particular point the fibers lying in a particular orientation appear to have the same angle to the longitudinal axis regardless of depth in the dermis. Removal of up to nine such layers in one location did not reveal a noticeable change in angle.

Fiber angles to the longitudinal axis range from 90° in the most anterior origin of the fibers where the fibers overlie the anterior origin of the epaxial muscle bundles, to near 0° where they approach the most posterior regions of the caudal fin. The majority of the fiber angles to the longitudinal axis in the measured region (A to O) range from 50° to 70°. Where the fibers cross the horizontal skeletogenous septum they change in angle in most cases. Fibers running dorsocaudal to ventrocranial below the longitudinal axis in the region from the anterior origin of the pectoral fins to the posterior free edge of the pelvic fins are significantly larger in nearly all cases than fibers running in either direction above or below the longitudinal axis in this region. Buckling of the skin occurs on the concave side of a swimming shark in this region below the longitudinal axis.

It is not known if the angles in this region specifically, or any other region, can change during muscular bending of the shark, or how much change of angle would be possible with the tight bonding of the fiber layers described. The buckling of the skin that did occur in the belly region of the swimming sharks could be a function of the fiber angles in this region, which are greater to accommodate the temporarily expandable gut. The skin could be slightly flaccid or loose when the gut is not full and hence be thrown into folds, and more taut when the gut is full.

Jarman (1961) while working with intermuscular bones of fishes concluded that in a block of muscular tissue which is undergoing unidirectional contraction there must exist some line at an angle to the direction of contraction that neither shortens nor extends when the muscle contracts. He found that there exist such lines oriented obliquely to the direction of contraction that lie at an angle of arctan $\sqrt{2}$ or approximately 55°. This proof can be extended to show that lines oriented obliquely on the surface of the contracting block (as compared to Jarman's lines inside the block) undergo minimum change when they lie at an angle of approximately 55° to the longitudinal axis of contraction.

Willemse (1972) constructed a simple model to represent one musculus lateralis and the vertebral column of the shark *Squalus acanthias.* The model consisted of stretched rubber tubing bound to a steel strip. To firmly bind the rubber tubes to the axis, loops of cotton thread were used. The angle that these loops of thread make to the direction of contraction is found to be important. If the thread is bound in loops almost parallel to the axis of the model they are found to have a small tying ability, transverse loops were found to have an excellent tying ability but bound loosely they allow a certain sliding of the contracting element along the resistant element, and bound tightly they restrict contraction by restricting the thickening that accompanies muscular contraction. A cotton thread lying at an angle of 55° to the direction of contraction has a good tying ability and exerts no restriction on the contracting element in its vicinity.

Referring to Table 3 one will note that the majority of the angles lie between 50° and 70°. It appears probable that fibers lie at such measured angles so as to remain unchanged in length during swimming and not impose any restriction on the swimming shark. Owing to the varying cross sectional shape of the sharks body and to such regions as the temporarily expandable gut region it seems reasonable to assume that the angles would not lie exactly on 55°.

The epidermis of sharks consists of a basal layer of cuboid cells, and numerous irregular layers of squamous cells (Stockard, 1944). The greater part of the skin being composed of the dermal collagen fibers. The skin is covered with small dermal denticles; the strength of the skin lying almost entirely in the dermal fibers.

Collagen fibers can be stretched by 10–20% of their length before they break; a great deal of this lengthening is due to the straightening of the fibers, and only about 9% to extension of the actual fibrils. The young's modulus for such fibers in human skin is about 10^{10} dynes/cm^2 (Alexander, 1968). This means that the longitudinal extensibility of collagen fibers and fibrils is not very great; otherwise, collagen fibrils require a high force to distend them (Elden, 1968).

Fujii (1968) believes that the primary function of this type of collagenous lamella is to strengthen the integument of an animal, protecting it against splitting under tensile force. This thick dermal region in sharks could have evolved in part as a means of mechanical protection against predation by other fish, the small placoid scales giving little protection against such things as other shark bites.

External protection in the teleosts may lie greatly in the relatively large scales and much less in the dermis. The numerous layers of collagen fibers, bound tightly by the described cross-over fibrils presents in sharks, a thick, strong, tightly bound protective sheath that would be resistant to puncturing or cutting by such things as other shark's teeth.

As thick as the stratum compactum may get in sharks, for instance *Ginglymostoma*—3.88 mm, the fibers lie at such angles that there is minimum restriction on the swimming shark. These angles vary throughout the shark itself, an angle being the function of the geometry of a particular region.

The bonding of the perimysial connective tissue fibers among themselves and with the stratum compactum fibers in the dermis suggests a firm and evenly distributed external anchorage for the body musculature of the shark. Contraction of the muscles and subsequent shortening of the myomeres could place a tensile force on the perimysial fibers attached to the dermis which would result in the distribution of tensile forces throughout the skin of the contracting region. The fact that no tension was observed in the fibers of the forceably bent shark may not indicate the same for a swimming shark, as forced bending and muscular contraction are different events with respect to shortening of the muscle.

Should a tension be set up in the dermal fibers in a region of bending then perhaps Willemse's model of the rubber tubing and steel rod would be applicable. In this case the dermal fibers would serve as a firm anchorage for the musculature without restricting contraction of the muscles, the dermal fibers would undergo minimal change in length during swimming, and the skin would also act as a mechanically protective layer.

Videler (1975) working on the teleost *Sarotherodon* (= *Tilapia*) *nilotica* found no evidence that during muscular contractions and bending of the fish that the dermal fiber angle changes. He postulates that during swimming the tension on the fiber system is equal in both dorsoventral and rostrocaudal directions resulting in no net change in angle of the fiber system. The dorsoventral tension in the fibers is generated by the contracting and bulging muscles on the ipsolateral side of the body, the rostrocaudal tension is due to the bending of the fin and fin rays due to the water's resistance, this bending exerts a tension on the dermal fibers inserted on the fin rays and produces a rostrocaudal tension. This system would result in the fibers not changing in length and the angles between the fibers remaining unchanged.

What Videler cannot explain is, despite this mechanism, how the tension in the skin remains constant during a stroke of the tail or otherwise, why the fibers do not buckle on the concave side of the bending fish. The system I describe may account for this supposed anomoly, in that, the fibers entering the tail lie at their optimum angle, in this case approximately 47°, so as to undergo minimum change in length and minimum tension change, yet act to support the fin rays.

Dermal fibers and the fins.—Teleost fins gain their support from the bony fin rays. Each segment of each fin contains a single ray, quite widely spaced, with a web of flexible tissue connecting the rays (Fig. 11). Each ray is composed of two half rays which branch distally. The two halves of the ray lie on either side of the most distal radial and are attached to the latter

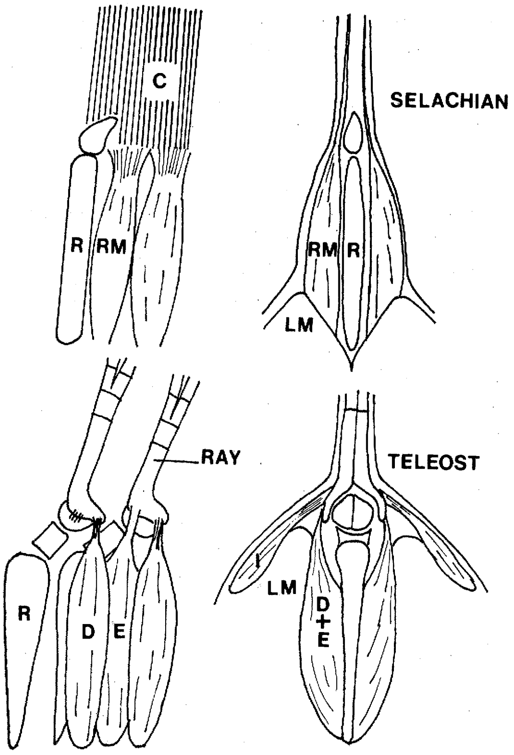

Fig. 11. The structure of the dorsal fins of a selachian (above) and teleost (below). Dissections, seen from left side, are shown on the left, transverse sections are shown on the right. C = ceratotrichia; D = depressor muscle; E = erector muscle; I = inclinator muscle; LM = longitudinal swimming muscle; R = radial; RM = radial muscle. From Alexander, 1974. With permission.

by ligaments. Muscle attachment occurs at the base of each ray (Alexander, 1974).

In the sharks the supporting elements of the fin membrane are flexible ceratotrichia. In each segment of the fin there are generally two cartilaginous radials. The more distal radial lies between two sheets of tightly packed ceratotrichia which extend to the edge of the fin. There is only one muscle on each side in each segment which inserts on the ends of the ceratotrichia by a broad tendon (Alexander, 1974). A single layer of stratum compactum fibers overlies and is attached to the ceratotrichia. They lie parallel to the direction of the ceratotrichia on the outer side of the latter (Fig. 3). Observations on fins other than the caudal fin are incomplete but it is believed that the fibers also overlie their ceratotrichia. Such a system would lend support to the flexible ceratotrichia, giving the fins additional support and rigidity.

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LITERATURE CITED

ALEXANDER, R. MCN. 1968. Animal mechanics. Sidgwick and Jackson, London.

———. 1974. Functional design in fishes. 3rd ed. Anchor Press Ltd., Essex.

ANDREW, WARREN. 1959. Textbook of comparative histology. Oxford University Press, New York.

BREDER, C. M. 1947. An analysis of the geometry of symmetry with special reference to the squamation of fishes. Bull. Amer. Mus. Nat. Hist. 88: 321–412.

BROWN, G. A., AND S. R. WELLINGS. 1970. Electron microscopy of the skin of the teleost, *Hippoglossoides elassodon*. Z. Zellforsch. Mikrosh. Anat. 103: 149–169.

ELDEN, HARRY R. 1968. Physical properties of collagen fibers, p. 283–344. *In*: International review of connective tissue research, Vol. 4. David A. Hall (ed.). Academic Press, New York.

FUJII, RYOZO. 1968. Fine structure of the collagenous lamella underlying the epidermis of the goby, *Chasmichthys gulosus*. Annot. Zool. Japan 41:95–106.

JACKSON, SYLVIA FITTON. 1968. Morphogenesis of collagen, p. 1–66. *In*: Treatise on collagen, Vol. 2: Biology of collagen, Part B. Bernard S. Gould (ed.). Academic Press, New York.

JARMAN, G. M. 1961. A note on the shape of fish myotomes. Symp. Zool. Soc. Lond. 5:33–35.

JOHNELS, ALF G 1950. On the dermal connective tissue of the head of Petromyzon. Acta. Zool. (Stockh.) 31:177–185.

JOLLIE, MALCOLM. 1962. Chordate morphology. Reinhold Publishing Corp., New York.

MOSS, MELVIN L. 1972. The vertebrate dermis and integumental skeleton. Amer. Zool. 12:28.

NADOL, JOSEPH B., JR. 1966. The development of an ordered array of collagen in *Fundulus*. Biol. Bull. 131:399–400.

———, JOHN R. GIBBINS AND KEITH R. PORTER. 1969. A reinterpretation of the structure and development of the basement lamella: An ordered array of collagen in fish skin. Dev. Biol. 20: 304–331.

SMITH, IAN C. 1956. The structure of the skin and dermal scales in the tail of *Acipenser ruthenus* L. Trans. R. Soc. Edinb. 63:1–14.

STOCKARD, A. H. 1944. A laboratory manual of comparative anatomy of the chordates. Edward Bros. Inc., Ann Arbor, Michigan.

VIDELER, J. J. 1975. On the interrelationships between morphology and movement in the tail of the cichlid fish *Tilapia nilotica* (L.). Neth. J. Zool. 25:143–194.

WILLEMSE, J. J. 1972. Arrangement of connective tissue fibers in the musculus lateralis of the Spiny Dogfish, *Squalus acanthias* L. (Chondrichthyes). Z. Morphol. Tiere. 72:231–244.

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Musculature of the Buccal Floor of *Bipes canaliculatus* (Reptilia: Amphisbaenia)

SABINE RENOUS

The present study of the myology of the buccal floor of *Bipes canaliculatus* emphasizes the important development of the M. sternomandibularis and of the complex M. cervicomandibularis, M. depressor mandibulae. This development can be presented as characters affected by the snake-like tendency and digging specialization. In comparison to other groups of limbless sauria the changes appear small, by reason of the persistence of the fore-limbs which take over the part played by the cephalic rostrum of other amphisbaenians; therefore, the anatomical modifications are more important at the pectoral level than at the buccal floor level. *Bipes* is a good example of two substitutions of function: the fore-limbs lose the locomotory function and are incorporated in a group of characters responsible for a new function in burrowing normally accomplished by the cephalic rostrum.

THIS report deals with four specimens of *Bipes canaliculatus* kindly donated by T. Alvarez who, in collaboration with M. R. Castañeda, published a thorough study of the appendicular skeleton of the genus (Castañeda and Alvarez, 1968). This species is peculiar to the Rio Balsas region, between the Mexican states of Michoacan and Guerrero. It is still poorly known; until 1964 there were relatively few specimens in museums.

Work concerning the amphisbaenians has been mainly osteological (Zangerl, 1944, 1945) and as yet provides little information on myology (Smalian, 1885), on the cranial muscles (Edgeworth, 1935) and of the muscles of the jaws (Haas, 1973). Gans has made numerous studies pertaining to the taxonomy of amphisbaenians (1960, 1964, 1965, 1967, 1971), locomotion and burrowing in these limbless vertebrates (1968, 1969, 1973, 1974) and their functional morphology (Wever and Gans, 1972, 1973).

The amphisbaenians are a homeogeneous group, showing marked specializations to subterranean living, and differ from the lizards and snakes in several characters (e.g. construction of the braincase). Vanzolini (1951) placed them into a single family, the Amphisbaenidae, with three sub-families: Amphisbaeninae, Rhineurinae and Trogonophinae. Gans (1969) postulated diphyletic origins of the group and, more recently (1974), recognized the prior taxa and a new one, the Bipedidae. *Bipes* is the only genus to have forelimbs.

In this work I present a morphological description of the buccal floor muscles without phylogenetic or functional interpretation. Some comparisons are made with, for instance, a scincid having a similar way of life.

DESCRIPTION

The scapular region.—From the first examination of the animal (Fig. 1) the elongated form of the body, the position of the forelimbs and, principally, their relative development compared with the body length are most striking. These limbs are attached ventrally and closely posterior to the head, thus reducing the normal length of the neck region among Squamata possessing anterior limbs. Upon removal of the skin, it becomes apparent that the episomatic musculature is very well developed in the ante-