

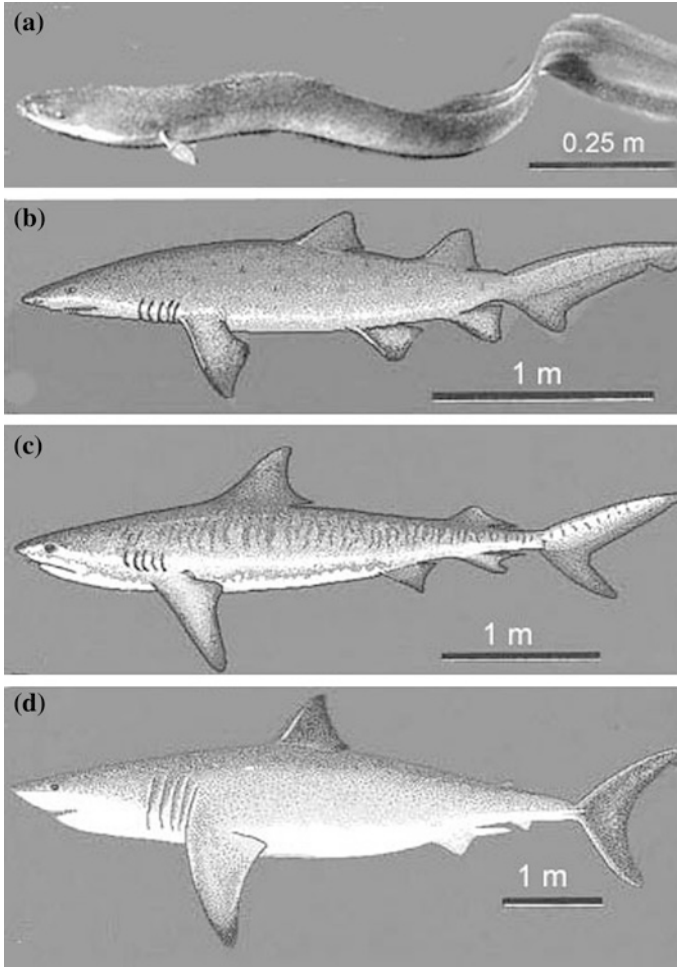
## Chapter 2

# Vertebrate Swimming

As we saw in the chapter on fishes in Volume 1, their success is reflected by the fact that the total number of fish species comprises more than half of the total number of approximately 55,000 recognized living vertebrate species. We ended Chap. 1 with a brief look at certain advances in our understanding of the hydrodynamics involved in vertebrate swimming. We will now look at the role the integument plays in the different swimming categories mentioned in Chap. 1 (Fig. 2.1) including special reference to the outer and inner dermis of sharks, a group with which we will start this chapter because it saw the first seminal research in this area among vertebrates. This will also be a suitable prequel to the group of fast swimming marine vertebrates, the thunniform swimmers.

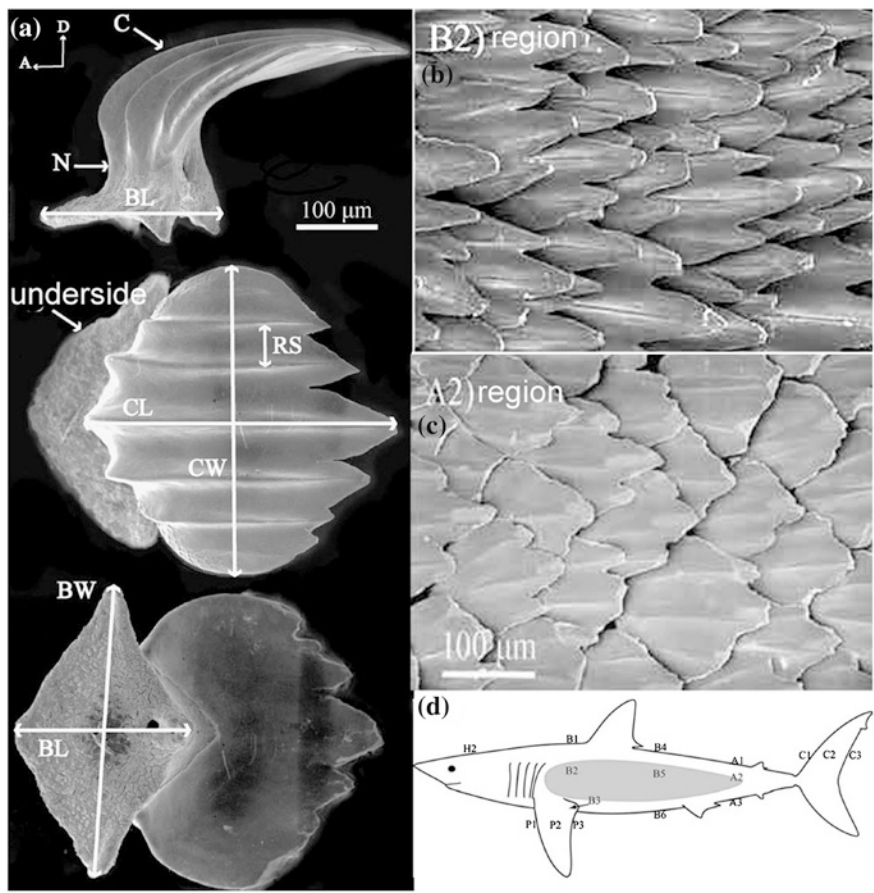
Most sharks use what may be described as an in-between mode of axial undulatory (anguilliform) and sub-oscillatory swimming. Some of the important developments with respect to the swimming dynamics were discussed in Chap. 1 and will not be dealt with any further here other than by way of comparison. Instead, we will stick to the two extreme swimming modes below, anguilliform and thunniform locomotion, and the crucial role that the superficial dermis and the deeper underlying dermis plays in them. We will start with the role of the superficial dermis, i.e., that region that gives rise to the scales in fishes (Volume 1). The scalation of sharks is an advanced example of how fish scales contribute to locomotion as seen through important research in the last 30 plus years. Further on we will see how the underlying dermis plays a similarly critical role in some of the fastest marine vertebrates in the oceans, albeit not involving scales, but rather a crossed-fiber collagenous architecture.

As shown in Volume 1, fish scales afford protection and help in hydrodynamic streamlining. However, during the last quarter of the 20th Century it was found that placoid scales may play a very specific role in the locomotion of sharks in controlling turbulence (discussed in Chap. 1). Here we look at the morphological characteristics that enable this function.



**Fig. 2.1** Differences in body profiles in an eel and three shark species reflecting different lifestyles and swimming potentials. **a** Eel, anguilliform. **b** *Carcharias taurus*, sub-anguilliform. **c** *Galeocerdo cuvier*, sub-carangiform or sub-oscillatory. **d** *Carcharodon carcharias*, thunniform or oscillatory

The scale crown has a very distinctive morphology that varies considerably, not only across the body but also among species (Fig. 2.2). The majority of scales on faster swimming sharks such as the shortfin mako, *Isurus oxyrinchus*, black-tip shark *C. limbatus*, and silky shark *Carcharhinus falciformis* have a series of parallel riblets (also termed micro-ridges, ridges, or keels) that run in an anterior–posterior direction, often terminating in cusps on the trailing edge of the scale (Motta et al. 2012). As mentioned in Chap. 1, Wolf-Ernst Reif and colleagues first proposed in the early 1980s that the highly specific orientation of these riblets and



**Fig. 2.2** A placoid scale. **a** Lateral, dorsal, and ventral views of a placoid scale (dermal denticle) from a 135.5 cm TL (total length) female blacktip shark *Carcharhinus limbatus*. Morphometric measures are indicated on each view (magnification 200X). Dorsal and anterior is indicated for the upper, lateral view. *B* base; *BL* base length; *BW* base width; *C* crown; *CL* crown length; *CW* crown width; *N* neck; *RS* riblet spacing. **b** and **c** From the B2 regions of the body respectively (see **d**). **d** Flank region (oval) and other parts tested. Modified from Motta et al. (2012)

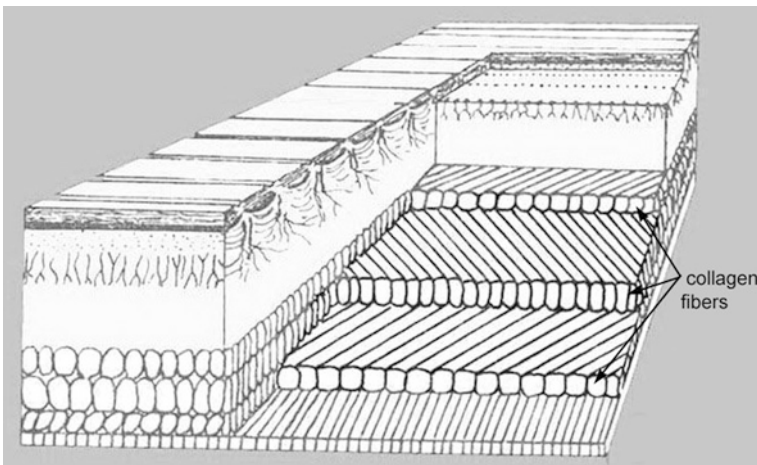
consistent height and spacing especially in fast swimming sharks have a hydrodynamic role, the understanding of which has since been supported by the use of supercomputers. The longitudinal riblets reduce drag because they impede the fluctuating turbulent crossflow near the wall, and in this way reduce momentum transfer and shear stress. Moin and Bewley (1994) and Moin and Kim (1997) showed by simulations of trajectories of marker particles in a turbulent water flow between parallel plates exactly how they work. The riblets appear to inhibit the motion of eddies by preventing them from coming very close to the surface (within about 50 μm). By keeping the eddies this tiny distance away, the riblets

prevent the eddies from transporting high-speed fluid close to the surface, where it would decelerate and sap the animals momentum (Chap. 1, Fig. 1.36).

In a morphological study of shark scales, Philip Motto and colleagues (2012) have shown specialization of scale morphology and patterns in the flanks of the fast thunniform shark, the short fin mako, *Isurus oxyrinchus* and the non-thunniform black tip shark, *C. limbatus*, which enables a new hypothesis on how reduction of drag might be achieved.

Motta et al. (2012) sampled scales in regions along the flanks of both sharks (Fig. 2.3). The placoid scales of the shortfin mako and blacktip sharks were anchored in the stratum laxum of the dermis with no obvious direct connection to the fibers of the stratum compactum. The attachment fibers of the scales in both species were almost exclusively collagen.

The authors found that the shortfin mako shark has shorter scales than the blacktip shark. The majority of the shortfin mako shark scales have three longitudinal riblets with narrow spacing and shallow grooves (Fig. 2.2b, c). In comparison, the blacktip shark scales have five to seven longitudinal riblets with wider spacing and deeper grooves (Fig. 2.2a). The relative riblet heights in the black tip were similar to those of the shortfin mako shark. The most significant finding is that *I. oxyrinchus*, one of the fastest swimming marine vertebrates, has a region of highly flexible scales along the flank with erection angles equal to or greater than  $50^\circ$ . This is in contrast to the scales on the other regions of the shortfin mako's body as well as all the scales of the black tip shark *C. limbatus*, which are not as erectable. The authors propose that the combination of a long crown length to short base length in *I. oxyrinchus* facilitates pivoting and erection of flank scales, which plays a key role in drag reduction that they hypothesize is passively driven by localized flow patterns over the skin.



**Fig. 2.3** The cuticle of the worm, *Ascaris lumbricoides*, showing collagen fiber layers. After Clark (1964)

## 2.1 The Deeper Dermis of Marine Vertebrates

### 2.1.1 *Non-thunniform Sharks*

With respect to the next section on the dermal fibers, although seemingly incongruous we will start with the more advanced form of locomotion, the thunniform mode, first, given that in the modern groups they evolved last. This can be explained by the chronology of the history of research and discoveries and, to a lesser extent, by the fact that the thunniform mode of swimming is in fact very old, having first evolved in the ichthyosaurs over 200 million years ago (Lingham-Soliar 1999, 2001; see Volume 1).

Perhaps the most significant study, which enabled much of the work in the area that followed, was that by Philip Motta. Motta (1977) investigated the dermis of a number of shark species by dissections and light microscopy. What he discovered was seminal—in several regions of the shark he found that the skin was comprised of multiple layers of oppositely oriented collagen fibers (Motta 1977), in some shark species as many as 45 layers of the dermis. While Motta thought that these layers of stiff collagen fibers served, at least in part, for protection and as an anchor for the musculature, he nevertheless asked some critical questions as to why the skin tension remains constant during each stroke of the tail and why the fibers do not buckle on the concave side of the bending. In fact he had touched upon the most important role of the fibers, which had never been described in a vertebrate animal before and so their function was very much a mystery. To understand the function of these cross-helically wound fibers one needs to go back in time to the late 1950s to a study by RB Clark and JB Cowey on perhaps the most unlikely of animals for an answer to our mystery, the humble nemertean and turbellarian worms. So important and influential was that study that we will break with the objective of this book of describing purely vertebrates, and in particular their integumentary systems, to describing the structure and biomechanics of the integument of these invertebrate animals.

In an elegant study incorporating both the biological and mathematical sciences, Clark and Cowey (1958) described how fibers that were largely inextensible in nemertean (from Greek myth, Nemertes, a sea nymph) and turbellarian worms, yet enabled the animals to extend and compress at will. The authors saw a complex problem that had to be resolved in these animals—the fibers enabled the body maximum stiffness and yet at the same time allowed the body all the flexibility necessary for the animal's vital movements in their locomotion. Put another way the inextensible fibers in the integument of animals enabled both stiffness and flexibility. This sounds like the stuff of which riddles are made. Indeed, in Greek myth the classic riddle was posed by a foul creature, the Sphinx, with a terrible death to those who failed to answer it. It might have fared better and had a very different result had it asked Oedipus instead, “What fibers are at once both extensible and inextensible?” Oedipus would undoubtedly have failed to answer it and have been promptly throttled and devoured by the creature and it would have saved a whole

lot of the messy business that followed. Instead Oedipus did answer the riddle posed by the Sphinx, resulting in its own destruction (see Sophocles' play (~430 BC)).

Yet, it was the answer that Clark and Cowey (1958) discovered and it involved a beautiful combination of biology and mathematics. The idea that hydrostatic pressure in many worms plays a role in invertebrate support and locomotor systems had been explored by many other researchers but it was not until the study by Clark and Cowey that the actual mechanism of how this was incorporated into the animal's locomotion was discovered. They found that the integument in turbellarian and nemertean worms was composed of regularly disposed inextensible fibers arranged in layers in alternate left- and right-handed geodesic helices extending around the body of the animal (Fig. 2.3 and Frontispiece).

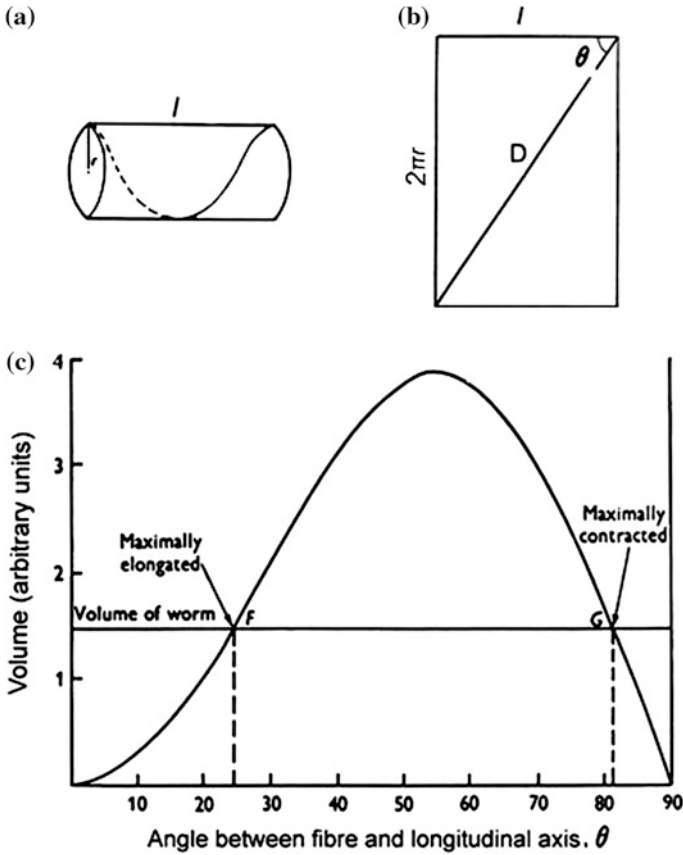
The model shows the worm as a fluid-filled tube stiffened by helical wrappings of inextensible fibers (Fig. 2.4a). Figure 2.4b show the section cut along the top and laid open, with just a single fiber represented. Although the fibers themselves are inextensible, changes of length of the body or parts of the body are permitted by a change in the angle of the crossed fibers exactly as the intersecting elements in a lattice or trellis. They demonstrated that in considering the fiber system alone there is a simple relationship between the inclination of the fibers to the longitudinal axis and the length of the system (Fig. 2.4c). In a cylindrical worm, e.g., as the inclination of the fibers changes so does the total volume the system can hold change, i.e., the volume varies according to the formula

$$V = D^3 \sin^2 \vartheta \cos \vartheta / 4\pi r$$

With extension, the segment's diameter and fiber angle both decrease; conversely, with segment shortening the fiber angle and diameter increase. If the segment maintains a circular cross-section, its volume,  $V$ , will vary, according to the curve in Fig. 2.4c.  $V$  decreases toward zero as  $\theta$  goes to  $0^\circ$  (a long, thin thread) or  $90^\circ$  (a flat disc), and it peaks at an intermediate angle of  $54.74^\circ$ . But an extensible worm, in most cases, does not change volume, so it cannot follow the curve. However, according to Clark and Cowey, "The system can always contain less than this volume if the cross-section is elliptical instead of circular" allowing a worm to adopt a flattened, elliptical cross-section as it changes length along a horizontal line of constant volume, as shown in Fig. 2.4c. The extremes of shortening and lengthening occur where this line intersects the  $V$  versus  $\theta$  curve and only here will the worm be circular. The greatest degree of flattening occurs when  $\theta = 54.74^\circ$ , also the angle where circumferential and longitudinal stresses in a pressurized cylinder balance (Wainwright et al. 1976). This is probably the reason why Clark and Cowey observed that a worm fully relaxed by anesthesia adopts a length where  $\theta \approx 55^\circ$ . In theory, a flatter worm should have a higher range of extensibility, because of its lower position on the plot in Fig. 2.4c, i.e., there is a greater range of lengths possible between the extremes bounded by the  $V$  curve.

Clark and Cowey (1958) stated that the helical bounding systems might be "widespread, if not general, in soft bodied, worm-like animals" but at the time even they had no way of anticipating the impact their findings would have





**Fig. 2.4** The cuticle of the worm, *Amphiporus lactifloreus*. **a** A unit length segment of a model worm, represented as a cylinder (radius  $r$ , length  $l$ ) wrapped by one full turn of an inextensible fiber having length  $D$ ; fibers with the opposite sense are omitted. The fibers follow the course of geodesics (i.e., the shortest line between two points on a curved surface). **b** The unit length in **a** cut along the top and laid open. **c** A curve representing the volume contained  $\theta$  by the cylindrical fiber system at different fiber angles  $\theta$ , showing the maximum occurring at  $54.74^\circ$ . Segments at low  $\theta$  are long and thin; at high  $\theta$  they are short and fat. The horizontal line represents the constant volume of the nemertean *Amphiporus lactifloreus*. It intersects the curve at F and G, which represent the maximum and minimum lengths, respectively. After Clark and Cowey (1958)

in biology, which extends to vertebrates as we will see in studies below (see Frontispiece).

In their book *Mechanical design in organisms*, Wainwright et al. (1976) promoted Clark and Cowey's (1958) model as a design principle in engineering and in nature, although solely in invertebrates. They recorded a number of studies that demonstrated the mechanical importance of the integument in a variety of invertebrates from insects to arthropods and mollusks. But it was not until soon after

Philip Motta's (1977) study on the cross-fiber structure in the dermis of sharks was published that Wainwright and colleagues (1978) were able to see that the design principle discovered in worms and thus far confined to invertebrates, might be equally relevant to large vertebrate animals.

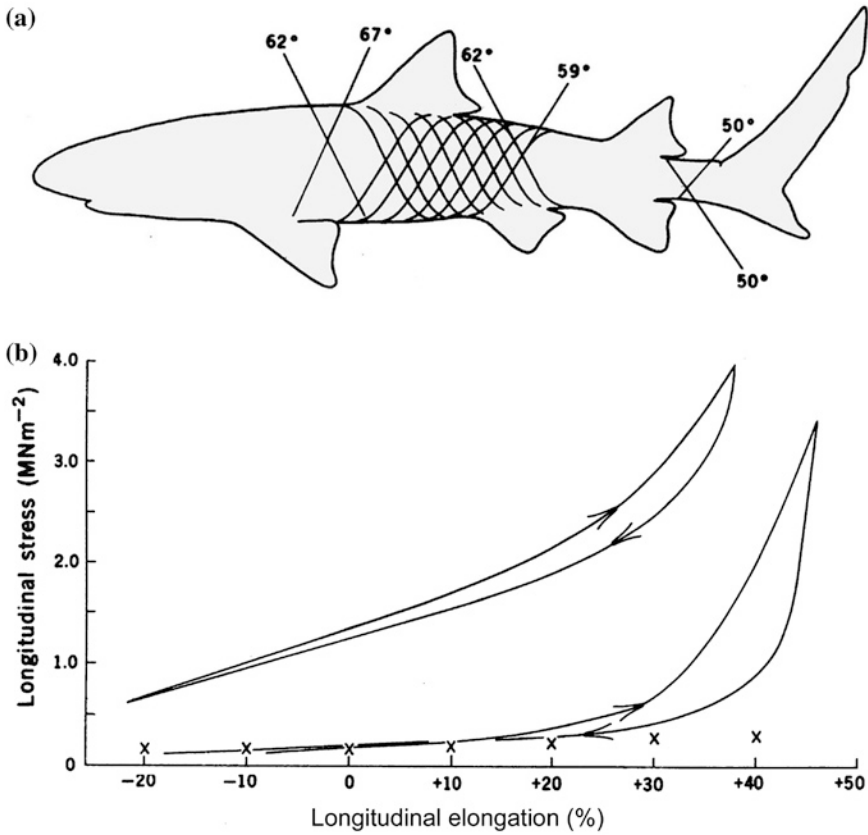
Wainwright et al.'s (1978) study published in the journal *Science* showed that during slow swimming the shark bent its body in left- and right-handed bends of 38 cm radius whereas during bouts of fast swimming tighter bends of 20 cm radius were produced and concomitantly the pressure rose from about 20 and 35–200 kN m<sup>-2</sup> during each tail beat, on both the concave and convex sides of the fish. The body stiffness achieved coincided with the angles made by the alternating left- and right-handed fibers with the long axis of the shark as seen in Philip Motta's study (Fig. 2.5a). This in fact could now be seen to conform with a common engineering principle with respect to thin-walled cylinders in which torsional stiffness can be enhanced by struts aligned at 45° to the cylinder's long axis (see Chap. 1) and that this was exactly how torsional stiffness was achieved in the sharks, i.e., collagen fibers in the skin wrapped at 45° to the body's long axis (Motta 1977).

The authors tested the shark skin in a biaxial testing machine and found that while pulling it longitudinally and holding a constant circumferential stress of 0.3 MN m<sup>-2</sup>, a great longitudinal extension of the skin occurred (Fig. 2.5b, lower curve). When they held circumferential stress at the fast swimming value of 2.8 MN m<sup>-2</sup> the stress in the unstretched skin at zero extension increased 13-fold and a given longitudinal extension required very much more stress than it does in the lower pressured slower swimming situation (Fig. 2.5b, upper curve).

To assess the torsional stiffness conveyed to the shark's body by the skin the authors performed load tests on the caudal peduncle with the skin intact and cut. They showed that the skin accounts for half the passive resistance to twisting despite the small percentage thickness (6 %) compared to the muscles. In addition, and this is important, unlike in the experiments on worms, this resistance was obtained in a dead shark, i.e., without hydrostatic pressure. Clearly, as the authors stated, the values obtained would be even higher in a living pressurized shark but nonetheless a high degree of resistance was possible without hydrostatic pressure (we will see situations with reduced internal pressure in Chap. 5). Wainwright et al.'s (1978) findings are extremely important and set the bench mark for future studies (including my own) on the biomechanics of the fiber structure of the vertebrate integument. The functional findings of their study may be summed up as:

- (1) Skin stiffness and the energy stored in shark skin depend on the amount by which the skin is prestressed by internal hydrostatic pressure at the time that it is extended.
- (2) The locomotory muscles of sharks as well as each muscle segment attaches to the skin over an area similar to that by which it attaches to the backbone and thus the skin acts as a tendon that increases the mechanical advantage of the locomotory muscle.





**Fig. 2.5** Helical fiber system. **a** Outline of a lemon shark (139 cm long) with some helical fiber angles indicated. **b** Longitudinal stress-extension behavior of skin from the lemon shark shown in Fig. 2.1. (Lower curve) The specimen was first stressed to  $0.3 \text{ MN m}^{-2}$  to simulate conditions in slow swimming. The crosses (x) are longitudinal stresses predicted by the relation: the square of the tangent of the fiber angle is equal to the ratio of the circumferential stress to the longitudinal stress. (Upper curve) The specimen was first stressed to  $2.8 \text{ MN m}^{-2}$  to simulate conditions in fast swimming. Rising and falling arrows indicate loading and unloading, respectively. Modified from Wainwright et al. (1978)

- (3) If the shark's skin is to transmit forces of contracting muscles to the tail, at rest the muscles have the same length and cross-sectional area, and the fibers in the skin make a  $60^\circ$  angle with the fish's long axis. Internal pressure is low and so is skin stiffness. To bend sharply as in fast swimming, the muscle on one side shortens and increases in cross-sectional area and girth. This causes fibers in the skin overlying the contracting muscles to increase their angle. The fiber angle controls the change in girth per unit change in length of the skin in concert with the surface of the contracting muscle. The changes in fiber angle imposed by the muscle cause the skin to remain taut in containing the muscle volume and to avoid wrinkling or loss of tension on the concave side of the fish.

- (4) Since skin stiffness is high, tensile forces applied to it are transmitted by it from the head to the tail. Since the backbone resists compressive changes in the fish's body length, contracting muscles pull on one side of the head and tail causing the fish to bend rather than to shorten.

The studies on shark dermal fiber structure paved the way for studies on the fastest swimmers in the oceans, the thunniforms.

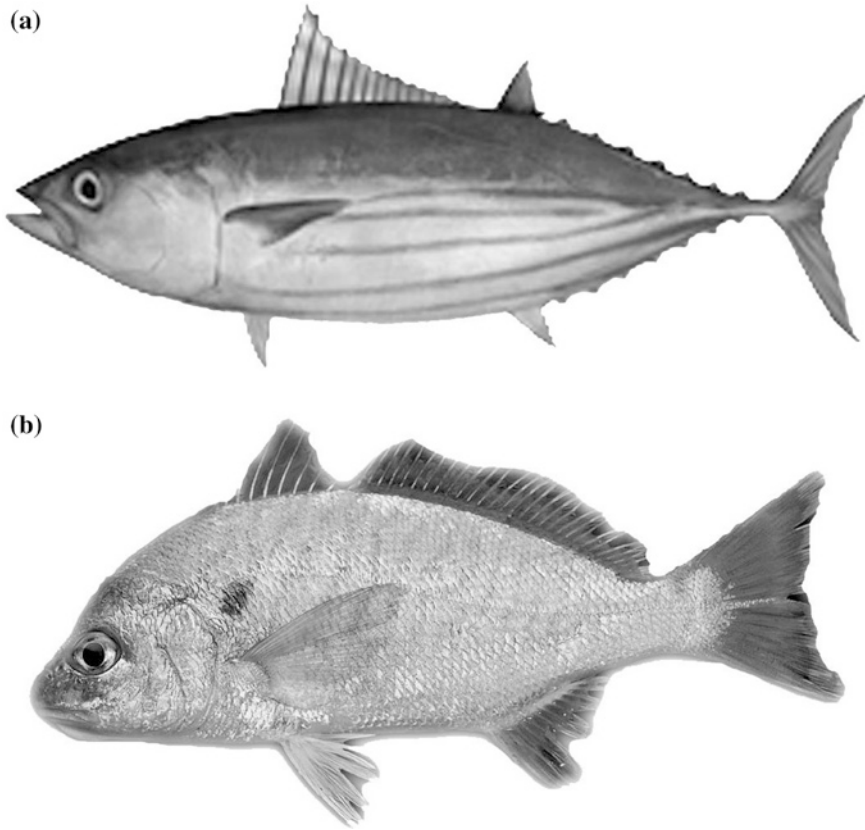
### 2.1.2 Thunniform Swimmers

The mathematician Sir James Lighthill (1975) categorized four groups of marine vertebrates as thunniform swimmers, tuna, lamnid sharks, dolphins and the extinct ichthyosaurs. Despite their disparate phylogenies, i.e., tuna and lamnid sharks are bony and cartilaginous fishes respectively, dolphins are mammals and ichthyosaurs are reptiles (see Chap. 1 and Volume 1), their apparent similarities have fascinated biologists and engineers alike for many years both in terms of biomechanics as well as the power of convergent evolution. However, convergent evolution in these animals was initially based on one criterion alone, body shape (including the caudal fin). It was through morphological investigations that at first were somewhat removed from questions of convergent evolution that we began to see deeper similarities in these animals. Among the four thunniform groups we will start with tuna.

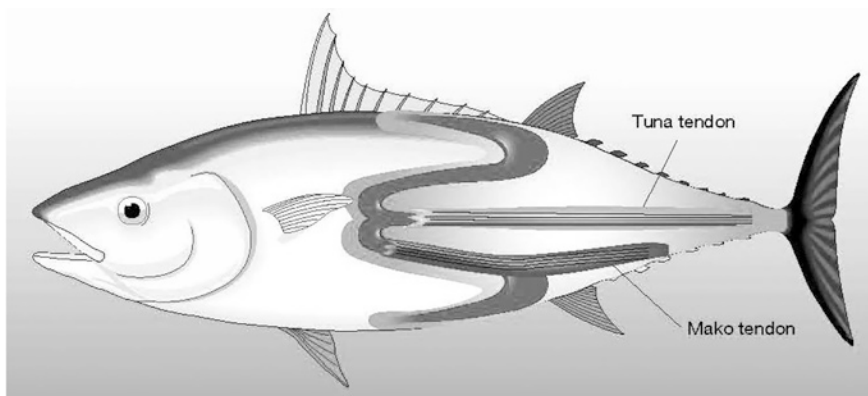
#### 2.1.2.1 Tuna Dermis

Following from Motta (1977) and Wainwright et al. (1978), the next breakthrough with respect to dermal fibers among fast vertebrate swimmers was in tuna, from which the thunniform swimming mode takes its name. Tuna arose some 40–60 million years ago at about the same time as the two other groups of extant thunniform swimmers, lamnid sharks and dolphins, possibly as a consequence of selection pressures for fast swimming as an effective part of predation at this time. Mary and John Hebrank (1986) investigated the skin of two species of tuna-like fishes belonging to the family Scombridae, the Norfolk spot, *Leiostomus xanthurus*, and the skipjack tuna, *Katsuwonus pelamis* (officially these do not belong to the genus of tuna, i.e., *Thunnus*, although they are commonly referred to as tunas (the skipjack most resembling them), they are scombrids. These are highly streamlined fish with a teardrop-shaped body and high aspect ratio tail (Fig. 2.6). The muscle forces that are anteriorly located are transmitted via the extremely narrowed caudal peduncle via a system of tendons (Fig. 2.7).

They found that in the Norfolk spot the skin is composed largely of a crossed-helical array of collagen fibers. Over most of the body of the fish these are oriented at angles of 45–80° with the long axis of the fish. The skin of *K. pelamis*



**Fig. 2.6** Scombrids. **a** Skipjack tuna, *Katsuwonus pelamis*. **b** Norfolk spot, *Leiostomus xanthurus*



**Fig. 2.7** The tendons connecting to the caudal fin has arisen convergently in the mako shark and tuna from the backward-pointing cone of connective tissue. Modified from Donley et al. (2004)

also contains a crossed-helical array of collagen fibers, although fewer fiber layers are present and fiber angles are generally in the range of 55–75°. To test the function of the fiber structures the authors performed uniaxial stress-strain tests on both species of tuna. They show that for both species the skin is most extensible in the longitudinal direction. For the Norfolk spot, the skin is stiffer in the direction of the fibers than in the circumferential direction, but for the skipjack tuna, the skin is of about the same stiffness in the circumferential direction as it is in the direction of the fibers.

The authors' results of biaxial tests of Norfolk spot and skipjack demonstrated that contraction of one side of the skin does not occur concomitant with extension of the orthogonal direction. Without this contraction tension cannot be transmitted by the skin down the length of the fish during swimming movements. This demonstrates that the skin of the spot and the skipjack do not behave as simple crossed-fiber systems, and are therefore incapable of transmitting forces down the lengths of these fishes or of acting as "external" tendons as found in sharks (above). The latter function is because a force applied to the skin can generate a greater bending moment than the same force applied near the backbone, the mechanical advantage of the axial musculature can be enhanced by pulling on skin that is capable of transmitting forces down the length of the fish (Wainwright et al. 1978). Hebrank and Hebrank suggested that this might be because sharks and eels (Hebrank 1980; see further on) are considered to be relatively primitive fishes and that both swim using fairly large amplitude waves of lateral undulation, whereas in their study of the structural features and mechanical properties of the integuments of two more advanced teleosts, the Norfolk spot and the skipjack tuna, they exhibit relatively small amplitude waves of lateral undulation and therefore the skin does not function as a giant tendon. Instead, for the spot and the skipjack, the crossed-fiber array of collagen seems to function primarily to keep the tough exterior surface of the fish smooth and free of kinks during swimming movements. A smooth surface is an important factor promoting hydrodynamic performance.

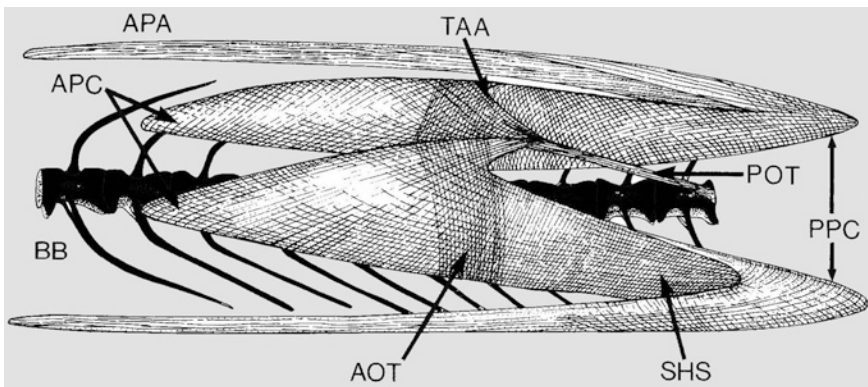
Hebrank and Hebrank (1986) also showed that the skin overlying the caudal peduncle (the very narrow region just anterior to the caudal fin) of the skipjack tuna is wrapped by dermal fibers at very steep fiber angles. This reinforcement is not seen in fishes that lack terminal tendons, such as Norfolk spot and eel (Hebrank 1980). Deep to the dermis, the tuna peduncle is also reinforced with a thick subdermal sheath, formed by myoseptal collagen fibers of caudal posterior pointing arms. We will consider this function further in the other thunniform swimmers.

### 2.1.2.2 Dolphin Dermis

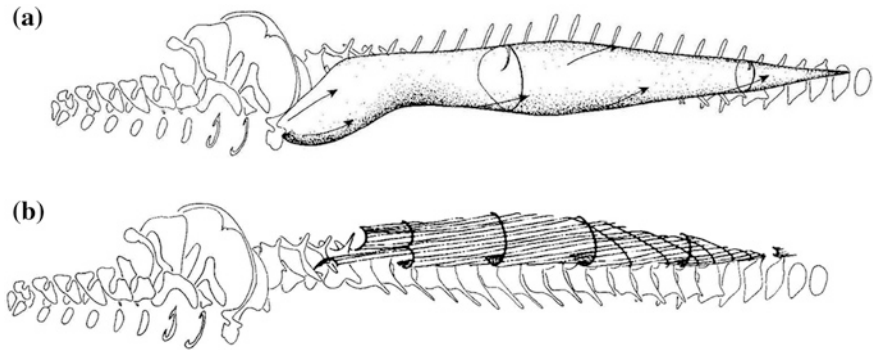
Our understanding of the role the skin plays in dolphin locomotion has been largely due to Ann Pabst at the University of North Carolina at Wilmington (Pabst 1996a, 2000). As mentioned, dolphins show the classic case of convergent evolution with tuna, lamnid sharks and ichthyosaurs. However, unlike tuna and sharks, but like ichthyosaurs (see further on), dolphins are secondarily adapted to aquatic

locomotion. As cetaceans (whales, dolphins and porpoises) they are distinctive from the other three groups in having arisen from terrestrial mammals. Part of that distinctiveness is reflected in their propulsion through the water—their caudal tail-stock and caudal flukes oscillate dorsoventrally, reflecting their terrestrial origins and locomotion, rather than laterally (side-to-side) as in the other three groups (even early land reptiles employed the side-to-side locomotion). Historically it was shown that the axial muscles, arranged in longitudinal tracts transmit forces via connective tissue “fabrics” of aponeurotic tendon sheets, and horizontal septa. Ann Pabst demonstrated that the skin played an important role in force transmission, i.e., that surrounding the axial musculature is a robust collagenous membrane which she named the subdermal connective tissue sheath (SDS). The SDS lies just deep to the blubber layer, is firmly anchored to the vertebral column and is formed by layers of collagen fibers that describe alternating right- and left-handed oblique angles relative to the long axis of the body, just as in the other animals described above (Figs. 2.8, 2.9).

Significantly, Ann Pabst found that the dolphin was modeled along the lines of a fiber-wound, thin-walled pressurized cylinder. With respect to mechanical functions, it was based on its cylindrical shape, a wall less than one tenth the radius in thickness, reinforced by two sets of fibers describing equal left- and right-handed fibers in alternating layers and, uniformly loaded by internal pressure. While elastin fibers were found associated with the SDS the predominant protein fibers were collagen. It was also found that fiber orientations, fiber diameters, and fiber layers and sheath thickness vary as a function of their position along the longitudinal



**Fig. 2.8** A scombrid myomere is a block of muscle, complexly folded into anterior pointing arms (APA), posterior pointing cones (PPC), and anterior pointing cones (APC). Each myoseptum is reinforced by two populations of collagen fibers—one wrapped circumferentially, the other longitudinally. Both populations of fibers coalesce in the main horizontal septum (the connective tissue structure that lies along the lateral midline and that connects the skin to the vertebral centra; not pictured here) to form obliquely oriented tendons. The circumferential fibers form anterior oblique tendons (AOTs), the longitudinal fibers form posterior oblique tendons (POTs). (BB represents backbone; TAA represents the triangular attachment area, the connection between the myomere and skin). Modified from Pabst (2000)



**Fig. 2.9** The dolphin longissimus muscle and the superficial tendon. Skeletal elements are shown as a series of cross-sections. **a** the longissimus, and its caudal extension, the extensor caudae lateralis. *Cross-sectional shape* of the muscle is indicated at various points, and *arrows* indicate the approximate angle of muscle fascicles. **b** The superficial tendon. *Thick transverse lines* indicate *cross-sectional shape* of the tendon. These tendon fibers change their orientation as they enter the subdermal connective tissue sheath (SDS); only the tendons that join the SDS on the ipsilateral side of the body are pictured here. These fibers approach the dorsal midline, become woven into the SDS and change their trajectories to insert on more caudal vertebrae. By permission of Ann Pabst (2000)

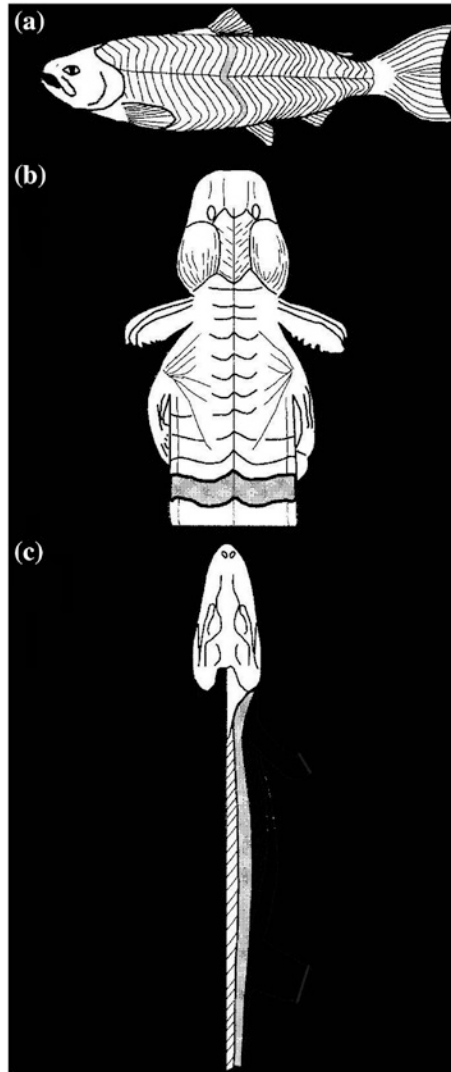
axis of the dolphin body. With respect to fiber angle, for instance, the forward and backward leaning fibers at the thorax are approximately equal but as one moves caudally the forward leaning fibers remain fairly constant but the backward leaning fibers become progressively steeper till near the insertion of the flukes they approach  $90^\circ$ . The sheath also becomes thicker caudally with an increase in the number of fiber layers. She also found that although there is a critical angle of  $60^\circ$  (McNeill Alexander (1987) demonstrated the functional role of the different fiber angles) at which the fibers may be strained and store energy, that when the animal bends this may differ in dolphins and that the vast majority of fibers may strain when the dolphin bends. Consistent with other animals, she found that the fiber morphology of the SDS resists torsion, prevents aneurysms and limits wrinkling when the dolphin bends. On the other hand her new model more accurately represents specific morphological features of the dolphin tapering cylinder. She predicted that the SDS also acts as a retinaculum for the terminal tendons of the axial locomotor muscles, and plays a role in maintaining the laterally flattened cross-sectional shape of the caudal peduncle (Chap. 1, Fig. 1.47b). The retinaculum is extremely important in marine animals with long tendons that have a tendency to “bowstring”, i.e., to lift away from the joints when they are pulled on by their muscles and when joints bend. A connective tissue band, reinforced with fibers at high angles (often perpendicular to) the direction of the tendon, as in the dolphin peduncle, is an ideal retinaculum. Pabst (2000) hypothesized that the body walls of vertebrate swimmers with narrow-necked caudal tailstocks would have to be reinforced against tendon bowstringing (this was investigated in the white shark, as we will see later (Lingham-Soliar 2005b)).



Pabst (2000) wondered if characters previously identified as convergent between cetaceans and tunas were predominantly external features. Her findings showed they were not and that comparisons extended much deeper such as the pattern of force transmission through the bodies of cetaceans and tunas and the musculoskeletal system with respect to: (1) Connections between axial muscles and peripheral, helically wound, connective tissue membranes that function to increase locomotor muscle performance. (2) A pattern of caudal intervertebral joint flexibility that controls caudal tailstock/peduncle movement. (3) Long, terminal tendons that function to control the angle of attack of the propulsive caudal fin/flukes. (4) A peripheral connective tissue membrane in the region of the caudal tailstock/peduncle, which is thickened and reinforced with steeply angled connective tissue fibers that function as a retinaculum.

Based on her findings, Pabst proposed that these convergent characters are “functionally significant design features” of steady swimming vertebrates. She looked at how the evolution of axial muscles involved changes in morphology, activation pattern and function as vertebrates made the transition from axially-powered (body) swimming to appendicularly-powered (limbs), terrestrial locomotion and vice versa. Interestingly, she found that dolphins and scombrid fishes do not share similar axial muscle morphologies. Although the design of the collagenous force transmitting structures are convergent, the morphology of the force generating axial muscle does not appear to be a functionally uniform design. In contrast to fish myomeres, the axial locomotor muscles of dolphins are organized into longitudinal tracts as is typical of mammals (reviewed in Pabst 1990) (Figs. 2.9, 2.10). On the other hand, regional patterns of vertebral flexibility in the common dolphin (Long et al. 1997) are similar to those described for tunas.

Long and colleagues (1997) found that the lumbo-caudal region appears to function as a rigid base of support for the muscles that act on the caudal tailstock and that caudal vertebrae 20 and 21 appear to function as a base for the highly flexible insertion of the caudal flukes. From these studies it is clear that tunas and dolphins possess convergent patterns of caudal vertebral flexibility. The serial arrangement of a stiff tail-base, intervening flexible spine, stiff caudal fin base, and compliant joint at the caudal fin insertion, appears to be a functionally significant design that controls the pattern of body bending in steady swimming vertebrates. In scombrid fishes, the five to six caudal-most myosepta form two sets of long, terminal tendons (Fierstine and Walters 1968; Westneat et al. 1993; Donley and Dickson 2000; Donley et al. 2004; Shadwick 2005). The great lateral tendon (GLT), which inserts on the caudal fin, is formed by the longitudinally oriented collagen fibers of the myosepta of anterior pointing cones. Likewise, the medial caudal tendon, which also inserts on the caudal fin, is formed by the longitudinally oriented collagen fibers of the myosepta of posterior pointing cones. The tendons transmit muscular force across the compliant joint at the base of the caudal fin and aid in controlling its angle of attack. Long, terminal, myoseptal-tendons are an apparently derived character for scombrids (Katz and Jordon 1997). In dolphins, the caudal extension of the longissimus, the extensor caudae lateralis, inserts onto the dorsal surfaces of the caudal-most vertebrae in the flukes, by way of seven



**Fig. 2.10** Evolution of epaxial muscles in vertebrates. **a** Fish axial muscles are organized into myomeres—a series of discrete, complexly folded units, separated by connective tissue membranes called myosepta. The *shaded area* represents a single myomere. Myomeres and myosepta connect directly to the skin as well as to the vertebral column, and function to produce lateral bending of the axial skeleton. **b** The epaxial muscles of most anamniotic tetrapods, as represented by salamanders, are myomeric in their organization, and most maintain their connections to the skin. The *shaded area* represents a single, *block-shaped* myomere. During both swimming and walking, the epaxial muscles function to produce lateral bending of the axial skeleton. **c** In amniotes, both the function and morphology of the epaxial muscles are changed. As is seen in the crocodile, the epaxial muscles are organized into three longitudinal tracts, most have lost their connection to the skin, and they function to stabilize the longitudinal body axis during appendicular locomotion. The shaded area represents the longissimus muscle. Adapted from Pabst (2000; see references therein)



**Fig. 2.11** Caudal peduncle of humpback dolphin dissected to show some of the muscle tendons as they enter the caudal fluke. Author's unpublished data

long, terminal tendons that are serially homologous to the superficial tendons (Pabst 1990). The extensor caudal lateralis is the only epaxial muscle to insert on fluke vertebrae, and aids in controlling the flukes' angle of attack. Thus, tunas and dolphins have converged upon a pattern of long terminal tendons that insert upon the propulsive caudal fin/flukes (Fig. 2.11).

This tendon morphology permits forces that are generated by large cross-sectional areas of more cranially-placed muscle (large anteriorly located muscle mass), to be transmitted and focused through the narrow-necked caudal peduncle—a functionally significant design feature of steady swimming vertebrates recognized as an adaptation to reduce drag. Fortuitously, it was possible to discover this design feature in the extinct member of thunniform swimmers, the 200 million-year-old ichthyosaur, *Stenopterygius*, which will be mentioned further on. We will consider these conditions in further detail later but first we will look at the lamnid or thunniform sharks with particular respect to structures that may reflect yet more instances of evolutionary convergence in the biology and biomechanics of the four groups of thunniform swimmers.

### 2.1.2.3 Lamnid Shark Dermis

Attention among thunniform vertebrates was next turned to the control surfaces of the white shark, *Carcharodon carcharias*, and the role of the dermal fibers in their mechanical performance (Lingham-Soliar 2005a, b). *C. carcharias*, along with the mako shark, *Isurus oxyrinchus*, belongs to a family of sharks (Lamnidae) using the fast, thunniform mode of locomotion (Donley et al. 2004), shared with as shown earlier just three other phylogenetically unrelated groups of large marine



**Fig. 2.12** Shortfin mako shark, *I. oxyrinchus* photographed from above as it swam close to the boat. Both the angle of photography and refraction of the water gives a more flattened impression of the animal but serve to emphasize the flattened plate-like caudal peduncle relative to the rest of the body. Photo permission of Lloyd Edwards

vertebrates, tuna (Scombridae), dolphins (Delphinidae), and the extinct ichthyosaurs (Ichthyosauridae; see below). Evolutionary constraints in the three extant groups of phylogenetically unrelated thunniform swimmers have imposed notable differences in the anatomy and biomechanics of the dorsal and caudal fins, principally connected with how stiffness is achieved. However, even a superficial examination in lamnid sharks shows the presence of a large, highly stiffened dorsal fin and a highly stiffened, high-aspect ratio (AR) caudal fin (and dorso-ventrally flattened caudal peduncle; Fig. 2.12), as opposed to all other sharks, with implications of very similar functions.

### Dorsal Fin

Despite significant work on the tail mechanics of sharks (Alexander 1965; Thompson 1976; Thompson and Simanek 1977; Wainwright et al. 1978; Graham et al. 1990; Ferry and Lauder 1996; Wilga and Lauder 2002, 2004), there are few studies that have examined the control structures of thunniform swimmers in any real depth, other than whether or not there was some kind of internal support system. Presence of a large, similarly shaped and similarly located dorsal fin in phylogenetically unrelated groups of cruising marine vertebrates (tuna, lamnid sharks, dolphins, and the extinct ichthyosaurs) underscores its apparent importance as a stabilizer. Evolutionary constraints, however, have imposed notable differences in the anatomy and structure of the dorsal fin in these groups. For instance, within

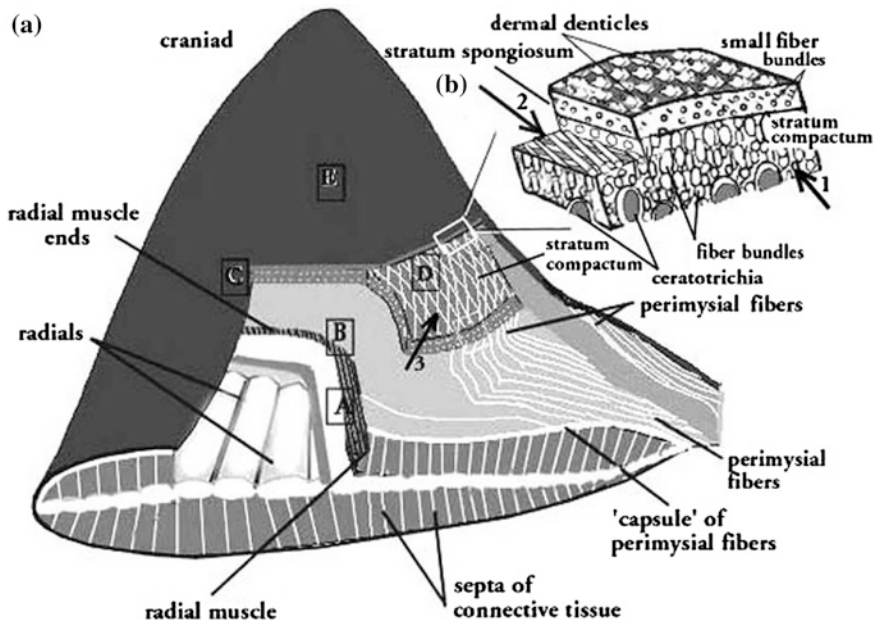
Teleostei, the dorsal fin in its derived condition, e.g., in fast-swimming perciforms, comprises two anatomically distinct portions: an anterior section supported by spines and a posterior section supported by soft rays (Drucker and Lauder 2001). In dolphins it is a de novo dermal structure, formed and supported only by connective tissue (Pabst 1996a) and in sharks it consists of soft, cartilaginous radials and highly flexible fin rays or ceratotrichia (Gans and Parson 1964).

Because little was known of the control structures in one of the most formidable predators in the oceans, the white shark, the possession of simple flexible, cartilaginous radials intuitively felt quite inadequate for maintaining a stiff dorsal fin comparable to that of the other extant thunniform swimmers. There had to be some other stiffening mechanism. Did the crossed-fiber structure discovered in the body of non-lamnoid sharks extend into the control structures of the white shark? However, Moss (personal communication in Motta (1977)) had earlier stated that only a basement membrane was present in the control structure of sharks and that the dermis was absent.

It is important to note that in studies such as this (Lingham-Soliar 2005a, b), before freezing for storage, that the carcasses are of freshly caught sharks (Cliff et al. 1996). Freezing has been found to have no effect on the tissue quality (Mann et al. 1990; Micozzi 1986; Gill-King 1997). Studies have investigated and dismissed the effect of freeze-thaw cycles on skeletal muscle including collagen fibers (Van Ee et al. 1998), articular cartilage (Tordonato 2003) and ligament tissue (Woo et al. 1986).

The internal anatomy of the dorsal fin in *C. carcharias* showed that the radial muscles extend less than half way up the dorsal fin and attach to the cartilaginous radials (Fig. 2.13) by perimysial connective tissue (PCT).

Contrary to Moss' (1972) findings in non-lamnoid sharks, transverse histological sections in the dermis in the dorsal fin of *C. carcharias* showed large numbers of dermal fiber bundles that extended from the body into the dorsal fin. However, they differed from those shown before in the body of sharks (Motta 1977). Here, they were organized in extremely elongated bundles (in cross-section, Fig. 2.13b, arrow 1) packed tightly together and became progressively more elongated deeper into the dermis. Most striking was the staggered formation of the adjacent bundles in the vertical plane, i.e., in a straight line from the fin surface to its interior. What this means is that they were not in distinct, well-organized layers of uniform depth, rather adjacent fiber bundles were staggered through the depth of the dermis, like a vertical brick work, some popping up and others down. This was in contrast to bundles of uniform cross-section occurring in neat rows (frequently demarcated by septa) as revealed in the dermis overlying the body of non-lamnoid sharks (Motta 1977). The close association of these tall bundles meant that the fiber bundles of the dorsal fin were packed to capacity in the dorsal fin of *C. carcharias*. Because Moss' findings were on non-lamnoid sharks, I also investigated two species of non-lamnoids, the tiger shark, *Galeocerdo cuvier*, a fairly competent swimmer (Fig. 2.1c), and the spotted ragged tooth shark, *Carcharias taurus*, (Fig. 2.1b), a relatively slow swimming species with two fairly low aspect ratio dorsal fins.



**Fig. 2.13** Schematic representation of the dorsal fin of *Carcharodon carcharias*. **a** The rectangle inserts A–E show sites from which transverse sections of the skin were taken. Note, sites A–E appear in this figure for convenience and represent only the locations of the dermal sections and are not intended to represent different orientations, levels, etc. Tangential sections were taken from sites A–C. Arrow 3 shows fibers in tangential view. **b** Representative transverse sections of the dermis taken identically in all five sites (A–E). Arrow 1 shows the plane of the transverse sections and arrow 2 the plane of the tangential sections. Lingham-Soliar (2005a), courtesy of Journal of Morphology, Wiley and Sons

First, both non-lamnoid species possessed significant amounts of dermal fibers, again contrary to Moss (1972) and, second, they were significantly different from those in the white shark. The findings in the three species examined were:

1. In all species the fiber arrangements of the dorsal fin occur in staggered formation, generally contrasting with the well-ordered rows previously found in the dermis overlying the body of the sharks.
2. Fibers are grouped in bundles of varying sizes, somewhat resembling skeletal muscle fasciculi.
3. Variations were found in stratum compactum fiber bundle profiles and densities in the three species with the most impressive concentration, distribution, and number of fiber bundle layers occurring in *C. carcharias*.
4. Fiber angles in the dorsal fin in the three species are  $60^\circ+$  to the long axis.
5. In the dorsal fin in all three species an orthogonal meshwork is formed by some layers of fibers but not by others.
6. Fiber bundles at the boundary just below the base of the dorsal fin are smaller in diameter and form an orthogonal meshwork.
7. In the caudal fin in *C. carcharias* fibers extend in parallel formation along the length of the dorsal fin in a number of clearly demarcated layers or rows.
8. In *C. carcharias* the fiber bundles in the caudal peduncle (close to the

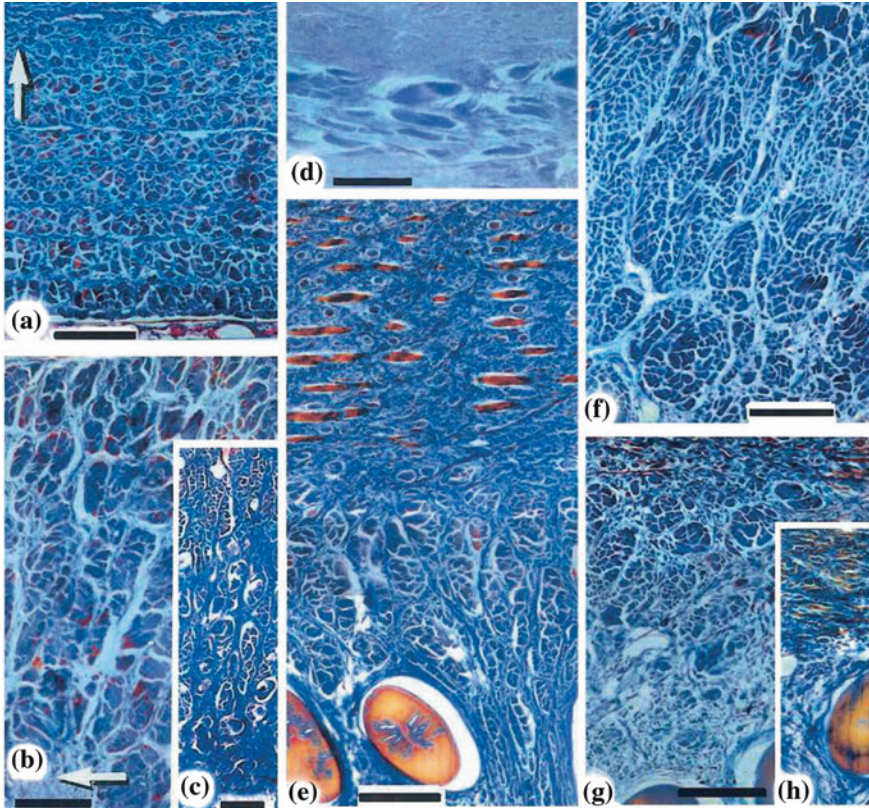


caudal fin) occur at angles in excess of  $60^\circ$  to the long axis of the animal. Fibers in layers are alternately left- and right-hand oriented and form an orthogonal mesh-work. 9. In the stratum spongiosum the fiber bundle profile (small size, sparse, and not grouped in larger bundles) is generally similar in all three species (Fig. 2.14).

With hindsight wisdom the fiber organization in the dorsal fin of *C. carcharias* shows exactly what one would expect of a dynamic stabilizer. Based on the fiber directions and close aggregations the indications are that they work like the riggings that stabilize a ship's mast. This means they have to allow an increase in tensile strength but without impeding the transfer of fiber tension from the body (Fig. 2.15). This is achieved principally in two ways: first fiber bundles are tightly packed in transverse section in more or less staggered formation but without being interwoven either as bundles or layers; and second fiber bundles are steeply oriented (in excess of  $60^\circ$ ) and strained (or pre-stressed), facilitating rapid transfer of tension from the body (see below). During fast swimming, when the problems of yaw and roll are greatest, hydrostatic pressure within the shark increases and the fibers around the body, including in the dorsal fin, become taut, thereby stiffening the fin. During slow swimming and feeding the hydrostatic pressure is reduced, the fibers are slackened, and the muscles are able to exert greater bending forces on the fin via the radials and ceratotrichia. In *C. carcharias* there is a trade-off for greater stiffness of the dorsal fin against flexibility.

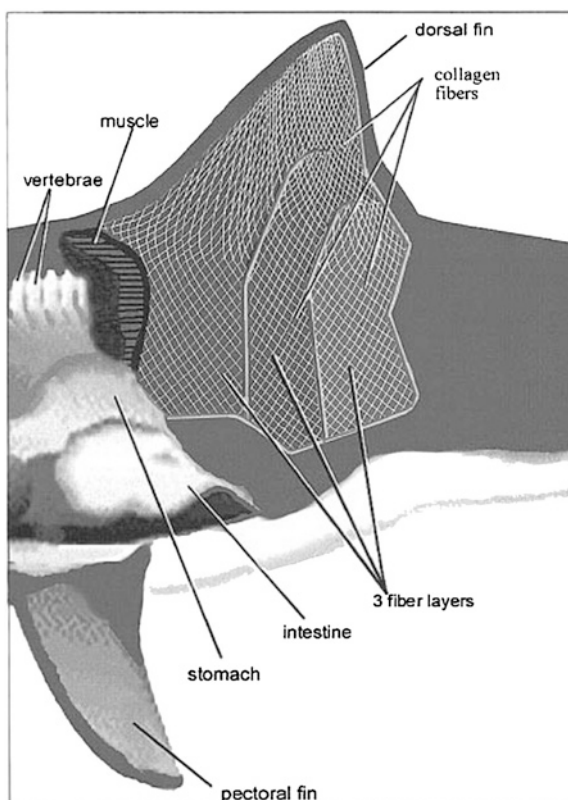
How critical are the fiber structure and mechanical characteristics of the dorsal fin to the lifestyle of *Charcarodon carcharias*? In a high speed swimming thunniform animal such as *C. carcharias* the powerful oscillations of the tail may induce recoil or lateral oscillations at the head. The latter could potentially diminish the net thrust by increasing viscous drag as the organism deviates from a rigid body (Nauen and Lauder 2002; Fish et al. 2003). In *C. carcharias* there are two ways in which the anterior recoil forces are reduced. First, by narrow necking and streamlining of the caudal peduncle (Lingham-Soliar 2005b; here, Chap. 1, Fig. 1.47a) this reduces the mass effect posteriorly during caudal fin oscillation and the corresponding recoil forces anteriorly (Blake 1983; Webb 1984; Reif and Weishample 1986; Fish et al. 2003). Second, by increasing the surface area around the center of mass by means of a tall and broad dorsal fin, this increases the added mass and inertia at the anterior end of the animal. The high angles of the fiber bundles act as reinforcement of the dorsal fin, comparable to the high angles of the fiber bundles in the caudal peduncle of dolphins (Pabst 1996a). In the lemon shark, tension on the shark's skin due to internal hydrostatic pressure was shown to increase with speed from  $\sim 20\text{--}35\text{ kN m}^{-2}$  to  $200\text{ kN m}^{-2}$  (Wainwright et al. 1978). It led to the hypothesis that this tension is transferred to the fibers on either side of the dorsal fin, which results in the fin becoming rigid (Lingham-Soliar 2005a). Thus, maximum stiffness occurs with maximum speed, and it is no coincidence that this also occurs when the problems of yaw and roll are most serious.

A highly stiffened dorsal fin is necessitated by the lifestyle of *C. carcharias*, a pelagic, high-speed swimmer at the top of the marine food chain (Randall 1983; Boustany et al. 2002; Froese and Pauly 2002). This lifestyle contrasts with that of *C. taurus* and *G. cuvier*. The more posterior position of the dorsal fins in



**Fig. 2.14** Representative transverse sections of the skin from the dorsal fin of *Carcharodon carcharias*, *Galeocerdo cuvier*, and *Carcharias taurus*. All sections are taken from the skin surface downward. Arrows at the upper and lower parts of the figure show top and craniad directions of the sections, respectively (refer to Fig. 2.13 for site locations). **a** Section from site A of *C. carcharias* RB 02057 (female) in which approximately nine distinct rows of dermal fiber bundles are present. Just visible above is the stratum spongiosum and at the bottom the connective tissue layer in which collagen fiber bundles are absent. **b** Site A of *C. carcharias* ZIN 02029 (male) in which the dense fiber bundles are staggered in formation. **c** Part of the stratum compactum of *C. carcharias* RBDS42 at site C in which numerous layers of fiber bundles are present. **d** About four rows of stratum compactum fibers are seen at site E in *C. carcharias* RBDS42. The fiber bundles have oriented with the long axis along the horizontal plane. Above is the stratum spongiosum and at the bottom connective tissue. **e** Site B in *Galeocerdo cuvier* in which the fiber bundles of the stratum compactum are already reduced. The upper half of the picture shows the stratum spongiosum in which small bundles of fibers occur within a collagenous matrix. The large yellow inclusions toward the bottom are ceratotrichia. **f** A major part of the stratum compactum fibers of *C. taurus* RB 02061 at site A showing densely aggregated fiber bundles in staggered arrangement. **g** By site B the stratum compactum fibers have dwindled to 2–3 rows. Above is the stratum spongiosum and below connective tissue with ceratotrichia just in view. **h** At site C there are no stratum compactum fibers in *C. taurus* RB 02061; only small fiber bundles may be seen in the stratum spongiosum. Scale bar in all figures except **d**, 0.25 mm. Scale bar in **d**, 0.5 mm. Lingham-Soliar (2005a), courtesy of Journal of Morphology, Wiley and Sons

**Fig. 2.15** A schematic view of the dermal fibers extending from the body into the dorsal fin of *Carcharodon carcharias*. The angles become much steeper in the dorsal fin ( $60^\circ+$ ) and the crossed-fiber meshwork is not always as evident as depicted in the scheme (see text). Lingham-Soliar (2005a), courtesy of Journal of Morphology, Wiley and Sons



*C. taurus* compared with *C. carcharias* and *G. cuvier* (see Fig. 2.1), exemplified in fish such as the northern pike, *Esox lucius* (Webb 1983; Webb and Weihs 1983), may enable more rapid acceleration from a stationary position, compared with slower starts in thunniform sharks (McGowan 1999), the former useful in ambush predation. A special ability to control its buoyancy and remain motionless by gulping air into the stomach (Bass and Ballard 1972) may also contribute to predation by stealth. Among sharks, *G. cuvier* spends considerable time swimming slowly in habitats that are varied (Tricas et al. 1981; Tricas and McCosker 1984; Heithaus et al. 2001; Heithaus and Dill 2002). Its dorsal fin is closely similar in shape and size to that of *C. carcharias*, but the dermal fiber structure suggests greater flexibility, which, in my view, may create less resistance during the strong lateral movements involved in underwater shake feeding (Frazzetta and Prange 1987; Frazzetta 1988, 1994), while stability is maintained by the pectoral fins (Springer 1961).

## Caudal Fin Dermal Fibers

The complex fiber organization in the dorsal fin of *C. carcharias* and the critical functional implications in a high-speed swimmer paved the way for a similar analysis of the caudal fin. We saw in Chap. 1 that the classic model of heterocercal tail function in sharks asserts that the tail produces a forward thrust directed in a line that would produce a turning movement around the center of balance: this would tend to raise the tail and drive the head downward in forward movement, the latter countered by lift generated by the pectoral fins (Alexander 1965) contrasting with Thomson (1976) and Thomson and Simanek's (1977) model, that hypothesized that the tail generates a reaction force directed through the center of mass. We also saw that recent studies using, e.g., digital particle image velocimetry (DPIV) on wake vortices in juvenile, benthic sharks, support the classic interpretation of heterocercal caudal fin function (Ferry and Lauder 1996; Lauder 2000; Wilga and Lauder 2002, 2004; Nauen and Lauder 2002; see Chap. 1) which was also at variance with the interpretations on how anterior balance is achieved (Fish and Shannon 2000).

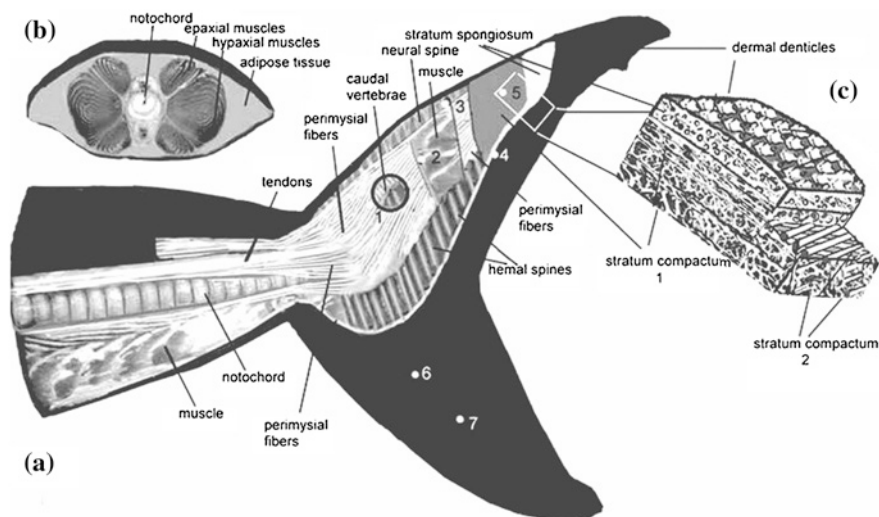
The above studies involved relatively slow swimming sharks and certainly cannot be used as a model for fast swimming thunniform sharks, which Wilga and Lauder (2002) acknowledge. The white shark is almost impossible to keep in captivity and hence upon which it is clearly impossible to perform DPIV analysis. Given such constraints, anatomical and biomechanical studies were performed on the control structures of the thunniform shark *Carcharodon carcharias* in an attempt to understand their locomotory potential (Lingham-Soliar 2005a, b) (Fig. 2.16).

Wainwright et al. (1978) investigated the role of the skin in swimming dynamics by twisting the entire tail and measuring the torque with the skin intact and excised and found that despite the thinness of the skin it contributed about 50 % of the tensile stiffness. However, because of significant differences in the lobe size and anatomy in the heterocercal tail of sharks it was considered important to test the two lobes in *Carcharodon carcharias* individually as well as the caudal peduncle (Lingham-Soliar 2005b).

The caudal peduncle in thunniform sharks such as *C. carcharias* is very different from that of other sharks. It is a highly modified, dorsoventrally compressed and rigid structure that facilitates the oscillations of the caudal fin (Fig. 2.12). Its stiffness appears to be principally achieved by a thick layer of adipose tissue ranging from 28 to 37 % of its cross-sectional area, reinforced by cross-fibered collagen fibers. Numerous overlying layers of collagen fibers of the stratum compactum, oriented in steep left- and right-handed helices (65° to the shark's long axis), prevent bowstringing of the muscle tendons, which lie just below the dermal layer (exactly as in dolphins) (Lingham-Soliar 2005b) (Fig. 2.16b).

With respect to gross structure, the bulk of the mass of the dorsal lobe of the caudal fin comprises the notochord (not present in the ventral lobe), perimysial fibers, muscles, and adipose tissue. The adipose tissue reinforces the leading edge of the dorsal lobe and contributes to an ideal cross-sectional geometry (tear-drop)

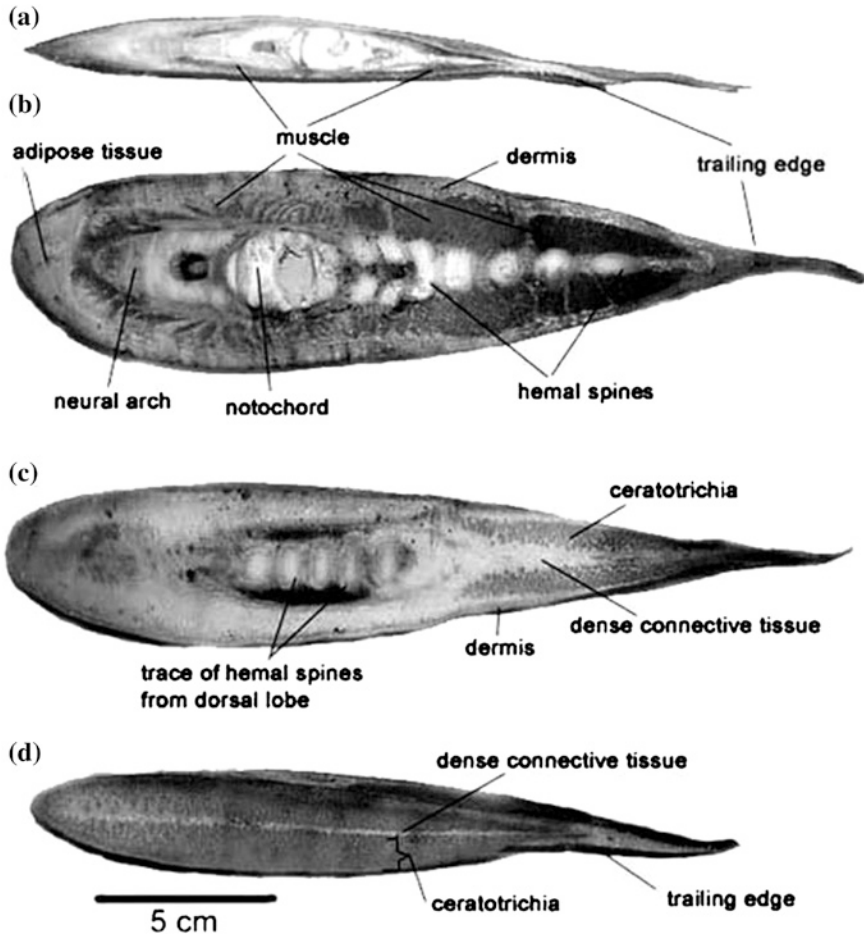




**Fig. 2.16** *Carcharodon carcharias*. Schematic representation of the caudal fin and caudal peduncle based on dissections. **a** Dissection showing, perimysial fibers, muscle, and notochord. Note, the caudal peduncle has been twisted ventrally to show the broad dorsal view. The hemal spines just intrude into the ventral lobe. Numbers indicate the sites from which transverse and tangential sections were taken. **b** Caudal peduncle transverse section taken from a point just anterior to the mid-length showing the adipose tissue, muscle, and notochord. **c** Schematic 3D block cut from the fin showing principally transverse (1) and tangential (2) views of the stratum compactum fibers. Lingham-Soliar (2005b), courtesy of Journal of Morphology, Wiley and Sons

consistent with an advanced hydrofoil (Figs. 2.16, 2.17a, b). In contrast most of the mass of the ventral lobe consists of the ceratotrichia or fin rays separated by thin partitions of connective tissue. At the core is a pith of gas-filled cells (Fig. 2.17c, d).

The dermal fibers of the stratum compactum of the caudal fin of sharks had not been investigated previously (Lingham-Soliar 2005b). Consistent with findings in the dermis overlying the body of other sharks (Motta 1977) the fibers of dorsal lobe of *C. carcharias* were found to occur in numerous distinct layers. However, the layers are more complex than in other sharks and reflect a hierarchical development, i.e., the fiber layers comprise thick fiber bundles with the thickest occurring deepest in the stratum compactum and diminishing in size toward the surface. Each of these layers alternates with and is separated by a single layer of fiber bundles, a formation thought to give stability to the stratum compactum and to enable freer movements of the fiber system. In tangential sections of the stratum compactum the fiber bundles in the dorsal lobe can be seen oriented with respect to the long axis of the shark at  $\sim 55\text{--}60^\circ$  in left- and right-handed helices. Because of the backward sweep of the dorsal lobe ( $55^\circ$  to the shark's long axis) the right-handed fibers also parallel the lobe's long axis. In the dorsal lobe, ceratotrichia are present only along the leading edge (embedded within connective tissue), apparently as reinforcement (Fig. 2.18).

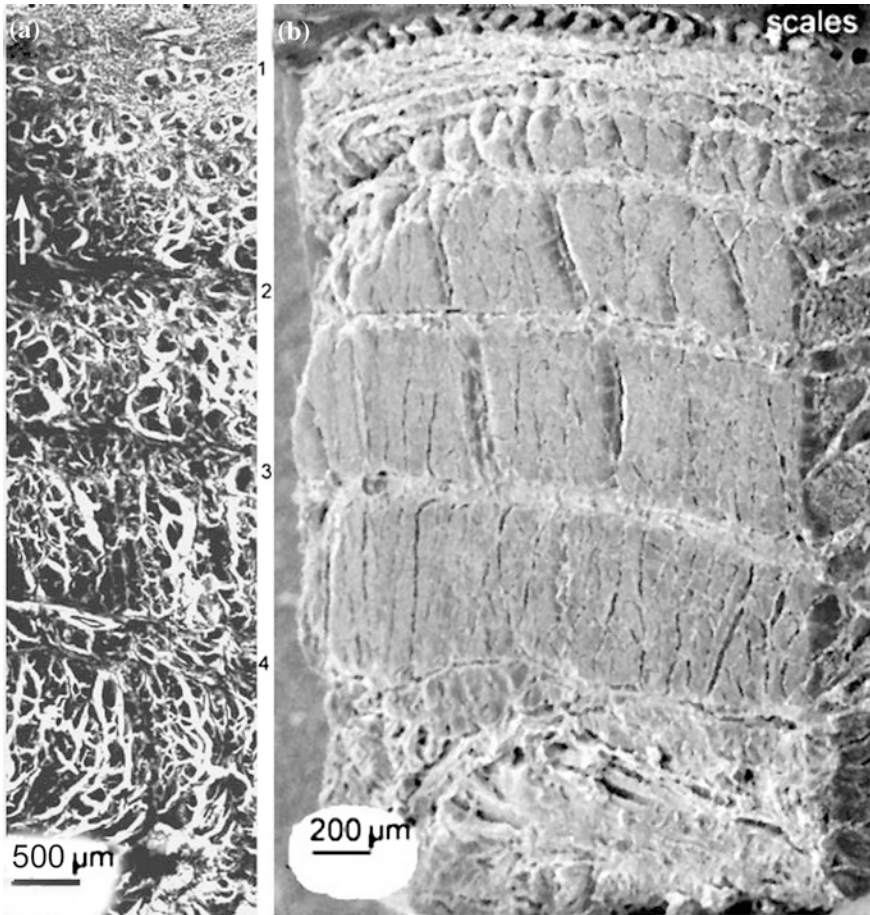


**Fig. 2.17** *Carcharodon carcharias*. Caudal fin cross-sections. **a** Approximate two-thirds span dorsal lobe. **b** Base dorsal lobe. **c** Base ventral lobe (hemal spines from dorsal lobe just intruding). **d** Approximate two-thirds span ventral lobe. Lingham-Soliar (2005b), courtesy of Journal of Morphology, Wiley and Sons

The dermal fiber bundles of the ventral lobe, viewed in transverse section, lack the well-ordered distinctive layers of the dorsal lobe, but rather occur as irregularly arranged masses of tightly compacted fiber bundles of various sizes, more resembling those of the dorsal fin. In tangential sections the fiber bundles are oriented at angles of  $\sim 60^\circ$ , generally in one direction, i.e., lacking the left- and right handed helical pattern. Below these layers of the dermis, dense layers of ceratotrichia extend virtually to the core of the fin and comprise a ‘honeycomb’ of air pockets (Fig. 2.19).

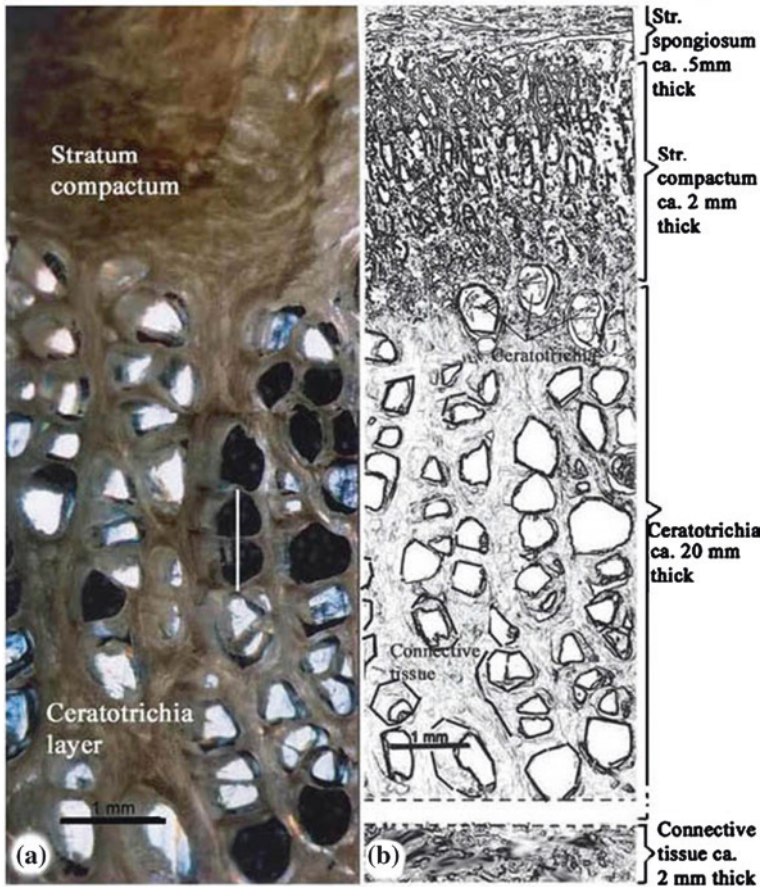
Tensile load tests on the skin of the caudal fin [by testing with skin intact and then with skin excised (see Wainwright et al. 1978)] indicate high passive





**Fig. 2.18** Dermal fibers of *Carcharodon carcharias*. **a** Transverse section. Eight layers of fiber bundles; four thick layers alternating with 4 thin layers (numbered 1–4) at one-third span. A further layer at the base is less organized and with a higher proportion of connective tissue. *Arrow* = vertical direction of section to the surface. **b** Similar section as **a** by scanning electron microscopy. **a** Modified from Lingham-Soliar (2005b) and **b** Authors unpublished data

resistance to bending. The shear modulus  $G$  showed that the skin's contribution to stiffness (average values from three specimens at radians 0.52 and 1.05) is 33.5 % for the dorsal lobe and 41.8 % for the ventral. The load tests also indicate greater bending stiffness of the ventral lobe compared to the dorsal. Overall, the anatomy and mechanics of the dorsal lobe of *C. carcharias* facilitate greater control of movement compared to the ventral lobe. However, I anticipate that with increasing speed and increased hydrostatic pressure in the dorsal lobe (the ventral lobe, unlike the dorsal, lacks a muscle and blood vascular system) the dorsal lobe

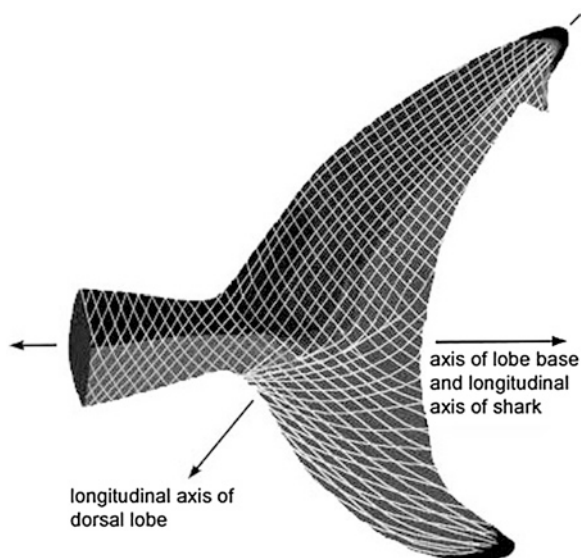


**Fig. 2.19** *Carcharodon carcharias*. Vertical section of the ventral lobe at one-third span under dichromatic light. Ceratotrichia. **a** Part of the dense layer of ceratotrichia (below the dermis) that extends virtually to the core of the fin. All white/bluish shapes are thin sections of ceratotrichia. The black shapes are where the thin sections have fallen out. **b** Scheme of vertical section of the ventral lobe, from the stratum spongiosum to the core, which is composed of a dense, irregular mass of connective tissues; only the upper part of the ceratotrichia layer is shown as indicated by stippled lines. Scale bar ~1 mm. Lingham-Soliar (2005b), courtesy of Journal of Morphology, Wiley and Sons

will match the static stiffness of the ventral lobe. The helical fiber architecture near the surface of the caudal fin is analogous to strengthening of a thin cylinder in engineering (see Chap. 1).

The detailed anatomical and morphological descriptions (Lingham-Soliar 2005b) were vital to the functional interpretations. High fiber angles along the span of the dorsal lobe are considered ideal for resisting the bending stresses that the lobe is subjected to during the locomotory beat cycle. They are also ideal for

**Fig. 2.20** Schematic interpretation of the stratum compactum fibers of the dorsal lobe of *Carcharodon carcharias* showing the fiber helices. Arrows show the two axes along which the fibers were examined and fiber angles based upon. Lingham-Soliar (2005b), courtesy of Journal of Morphology, Wiley and Sons



storing strain energy during bending of the lobe and consequently may be of value in facilitating the recovery stroke. The higher shear modulus in the ventral lobe may be explained by absence of vertebral support. The air filled cells in the middle of the ventral lobe may also be of functional significance (Fig. 2.19). For instance Dawson and Gibson (2006) who investigated the biomechanics of hedgehog and porcupine quills, which have compliant cores found optimization or improvement in the load ratio and moment ratio in shells with a honeycomb or foam core over an equivalent hollow shell. Overall both the compliant core (ventral lobe) and complex fiber structure of the dorsal and ventral lobes of the caudal fin and caudal peduncle of *C. carcharias* provides a realistic potential for an elastic mechanism in the animal's swimming motions and consequently for energy conservation (Alexander 1988; Pabst 1996b) (Fig. 2.20).

#### 2.1.2.4 Ichthyosaur Dermis

Modern studies on the extant thunniform swimmers, lamnid sharks, dolphins, and tuna help explain many of the complexities of structure and mechanics connected with high speed aquatic locomotion that were previously unknown. However, one group of extinct marine vertebrates, included as we said earlier among the thunniform swimmers, were the ichthyosaurs, albeit based purely on external characteristics, body and tail shape (Lighthill 1975). According to the modern studies that showed the importance of internal anatomical characteristics, particularly with respect to the dermal fiber structure and chemistry, no more than speculation on similarity of swimming locomotion with extant thunniform swimmers could

now be made. Hence, similar definitive evidence as found in modern-day thunniform swimmers was needed if more conclusive comparisons were to be made. A search for ichthyosaur soft tissue, which might hold some of these answers, was necessary.

The first problem that required an answer to the question referred to earlier, was there direct muscular control of the caudal fin in Jurassic ichthyosaurs or were nearly all the muscle fibers lost and the cones almost completely tendinous as in tuna and dolphins? Among the numerous ichthyosaur specimens examined, one appeared to provide some of the answers, a specimen of *Stenopterygius*, housed in the Geology Museum at Tübingen University (Fig. 2.21). It was possible to identify in the preserved soft tissue, structures that were near spindle-shaped in the region just anterior to the caudal fin and to reasonably conclude that these cone-shaped structures formed part of a tendinous sheath, which was apparently derived from myosepta (associated with the myomeres) and that it provided the basis in ichthyosaurs for a caudal tendon system (Lingham-Soliar and Reif 1998) (Fig. 2.22a, b), as demonstrated by Fierstine and Walters (1968) in tuna.

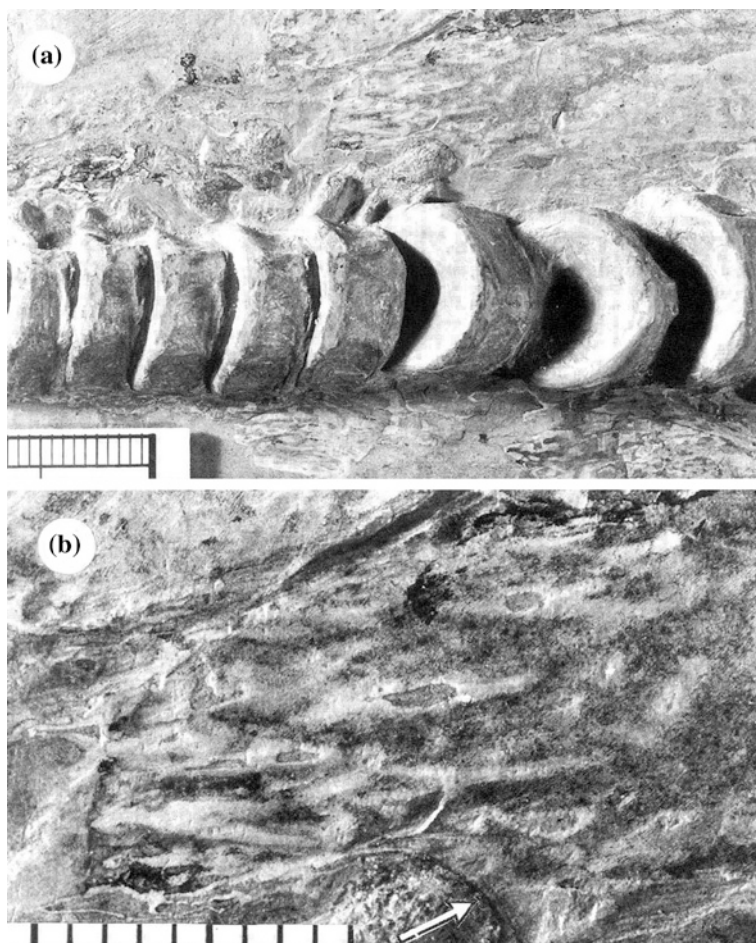
The next question, closely associated with narrow-necking of the region anterior to the caudal fin was whether or not a caudal peduncle, as in the white shark and dolphins, was present so as to enable a constant, high angle of attack of the caudal fin during the beating cycle. In a lateral beating cycle as in ichthyosaurs, the caudal peduncle if present would have been flattened dorsoventrally as in the white shark (Fig. 1.47a) and mako shark (Fig. 2.12). The odds were against identifying such a structure because virtually all Jurassic ichthyosaurs are laterally compressed during preservation. However one specimen that I was able to examine, *Stenopterygius* R 457 (Senckenberg Museum, Germany) showed a hint of dorsally displaced soft tissue in the peduncular region suggesting strong circumstantial evidence of a thickened lateral keel that had been twisted slightly vertically during lateral compression and apparently in consequence had displaced the vertebrae ventrally (Lingham-Soliar and Reif 1998; here Fig. 2.23).

Probably the most significant investigation involved whether or not Jurassic ichthyosaurs had a crossed-fiber architecture of the dermis comparable with that of the extant thunniform swimmers. The first clue to the possibility of a crossed-fiber



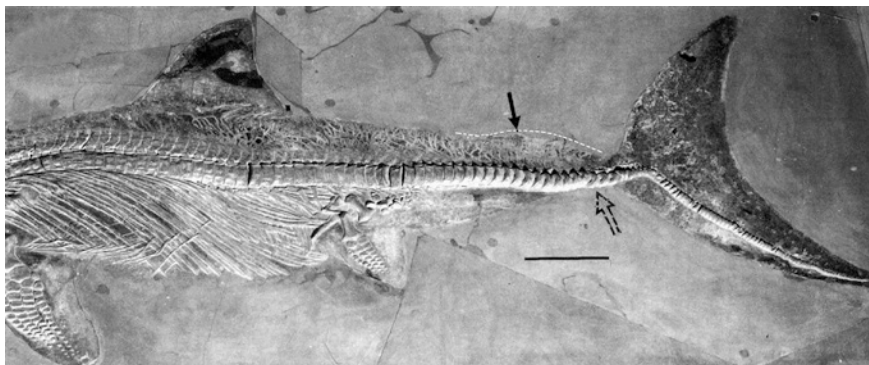
**Fig. 2.21** *Stenopterygius quadricissus* Re 1297/1 (Department of Geology, Tübingen University). Preparation is of the *right side* shows the lateral and part of dorsal surface. Scale bar = 25 cm. Lingham-Soliar and Reif (1998), courtesy of Neues Jarbuch (abh)





**Fig. 2.22** *Stenopterygius quadricissus* Re 1297/1 (Department of Geology, Tübingen University). **a** Part of exposed layer of tissue above vertebral 'peduncle' showing phosphatized fibers and a further layer of fibers is also visible below the vertebrae. **b** Detail of phosphatized fibers. Lower part of figure shows ruptured overlying tissue that is folded back (arrowed). Scale bar = 1 cm. Lingham-Soliar and Reif (1998), courtesy of Neues Jarbuch (abh)

architecture came from an ichthyosaur specimen, GLAHM V1180a, housed in the Hunterian Museum of the University of Glasgow. This specimen was identified as *Ichthyosaurus*, from the Lower Lias of England, which lived about 200 MYA (Lingham-Soliar 1999). Only the skull was preserved in a mudstone nodule but, fortuitously, this specimen showed traces of preserved skin (Fig. 2.24). This is not to be confused with many other ichthyosaur specimens from the world famous lower Jurassic Posidonia shale of southern Germany with so-called soft tissue preserved. Frequently, they are no more than decayed and transformed soft tissue



**Fig. 2.23** *Stenopterygius quadricissus* SMF R457. Dorsolateral view of meshwork of filamentous fibers over dorsolateral surfaces of the body. Because of slight dorso-lateral compression the fleshy outline of the caudal peduncle is visible. Scale bar = 25 cm. Lingham-Soliar and Reif (1998), courtesy of Neues Jarbuch (abh)

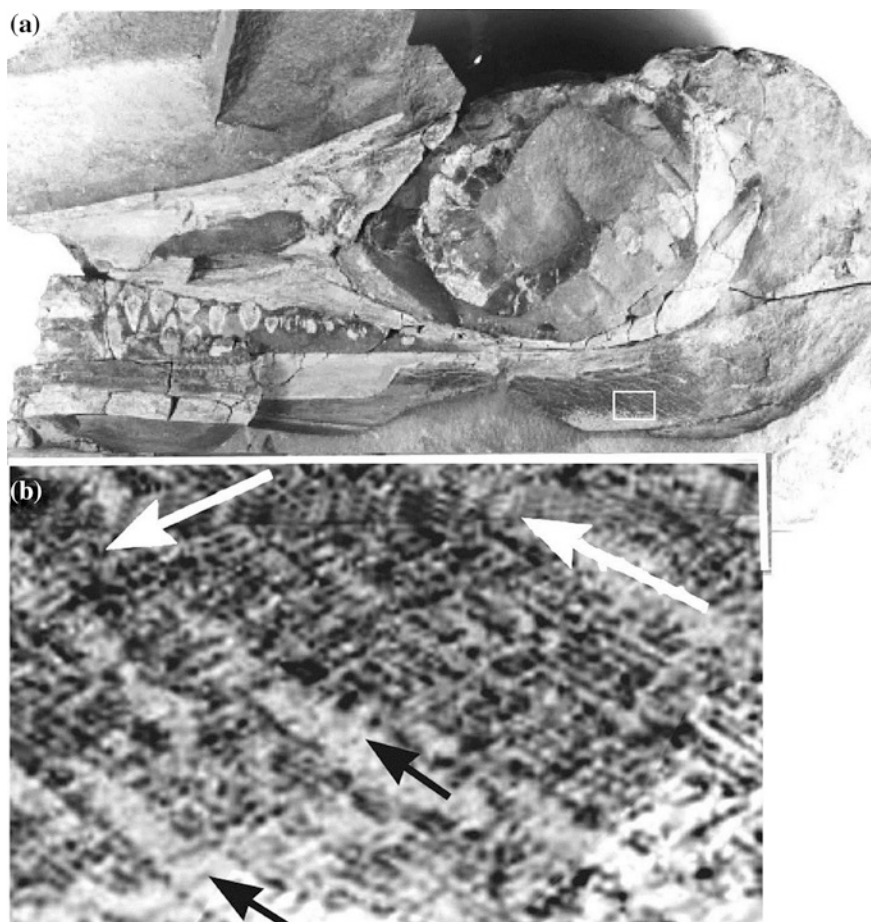
that may simply outline the body as a black carbon-like film, with little organic matter preserved including skin fibers. The Hunterian specimen shows actual preserved skin fibers overlying the jaws. Significantly, two layers of dermal fibers are revealed, which, despite erosion, show a crossed-fibered arrangement (Fig. 2.24b, white arrows) strikingly similar to that of tunas, dolphins, and sharks (Lingham-Soliar 1999). Note, the black arrows show patches of tissue (not individual fibers) that in an earlier study (Delair 1966) had mistakenly been identified as thick fibers.

However, because the fibers were found solely on the jaws it was not possible to state other than by speculation that they were found over other parts of the body as in the modern thunniform swimmers. This was critically important, because of the functional significance with respect to high-speed swimming (also see Volume 1).

Many specimens were examined in some of the best collections in the world, among which two ichthyosaurs specimens showed potentially viable soft tissue preservation over the body. They both belonged to the late Jurassic species *Stenopterygius quadricissus* and both were fossilized in the Posidonia Shales of southern Germany. Specimen PMU R435 was housed in the Uppsala Museum in Sweden and the other was specimen SMF R457, mentioned above. They were both coincidentally prepared by one of the finest fossil preparators in the world at the time, Bernard Hauff. These findings were described in Volume 1. Figure 2.23 shows some of the best preserved crossed-fiber architecture over large areas of the body in SMF R457 (the largest of which, up to 1 mm thick, are visible to the naked eye).

Fibers were identified in three size classes based on thickness and in different levels of the integument over virtually the entire surface of the body of the three ichthyosaur specimens named above (Lingham-Soliar 1999, 2001). The thickest fibers were located deepest in the skin and the thinnest in the outermost layers. However, this was the first such record of a hierarchical fiber architecture seen in



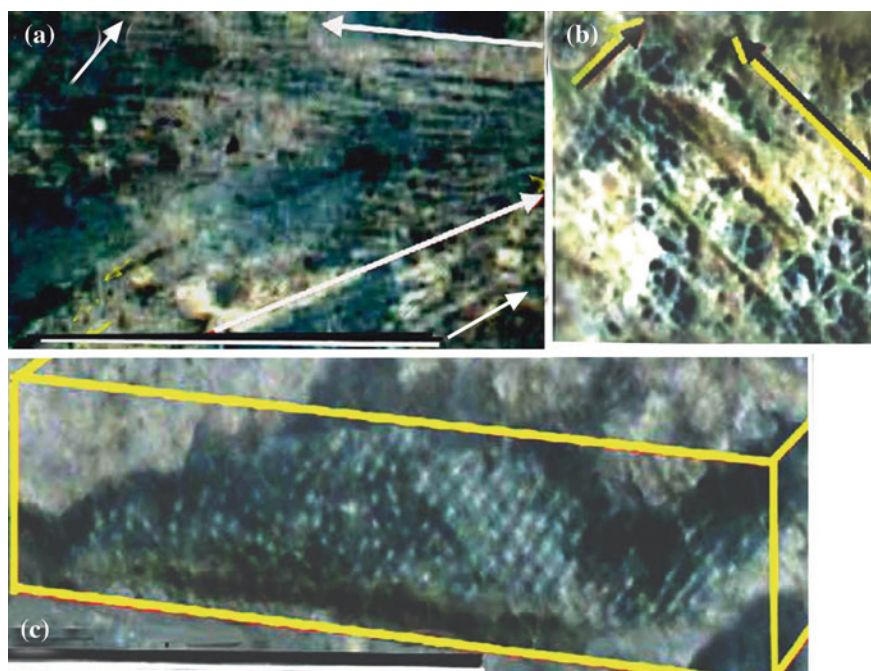


**Fig. 2.24** *Ichthyosaurus* GLAHM V1180a housed in the Hunterian Museum of the University of Glasgow. The specimen shows crossed-fiber architecture in the lower jaws. **a** The head preserved in a mudstone nodule. **b** A section of two layers of oppositely oriented fibers, fairly decomposed/eroded. Lingham-Soliar (1999) courtesy of the Royal Society of London

the integument of any vertebrate extinct or extant (Lingham-Soliar 2001). It was not until a few years later that a similar hierarchical structure of fibers in the dermis of the white shark, *C. carcharias*, as shown above, was found (Lingham-Soliar 2005b). The system comprised an architecture of oppositely oriented fibers in alternative layers just as they are in extant thunniform swimmers. The fiber angles varied over the body from between  $25^\circ$  and  $70^\circ$  to the long axis of the animals, which coincided with different amounts of stress in different regions of the body. Thus the fiber structure in Jurassic ichthyosaurs strongly suggested another important criterion of thunniform locomotion, namely a means for a highly stiffened body as demonstrated in extant thunniform swimmers (Lingham-Soliar 1999, 2001).

The next task was to examine the dermis overlying the dorsal and caudal fins and determine whether or not the ichthyosaur dermis aided in their biomechanics as established in sharks. The tail in both groups of animals had particular significance, given that ichthyosaurs, like sharks have vertebral support in just one of the caudal fin lobes, the lower (the upper in sharks).

*Stenopterygius* SMF 457 again proved invaluable, this time in resolving the fiber architecture in the dermis of the dorsal and caudal fins (2.25). Three major types of fiber orientations were shown in the dorsal fin of *Stenopterygius* of SMF R457 (Lingham-Soliar and Plodowski 2007) (Fig. 2.25a, b). In the first, alternating oppositely oriented fibers at the lower posterior part of the fin were oriented at low fiber angles that apparently allowed greater freedom of fiber movements and facilitated reorientation toward a stress axis (Naresh et al. 1997). This fiber pattern is similar to that observed in the white shark dermis (Lingham-Soliar 2005a, b). In the second, stiffness in the lateral plane is achieved by fibers that parallel or orient



**Fig. 2.25** Dorsal and caudal fin crossed-fibers in *Stenopterygius quadricissus* SMF 457 in the Senckenberg Museum in Germany. Dorsal fin. **a** High-tensile fibers near the fin base in three to four layers, two show low fiber angles and one, high. **b** Left- and right hand-oriented fibers toward the midpoint of the dorsal fin. Fibers occur in steeply angled right- and left-hand helices in several layers (arrows show main fiber directions). **c** Fibers in the caudal fin dorsal lobe (lacking vertebral support), exposed in transverse section (almost 90° to the surface) but also sheared in places at about 45° to the surface, occur as a unique 3-D image. About eight layers of fibers oriented at about 45° (right-handed) to the ichthyosaur's long axis can be seen. Scale bar in **a**, **c** = 1 cm (see Lingham-Soliar and Plodowski 2007 for figures on all seven zones investigated)

at steep angles to the long axis of the ichthyosaur (Fig. 2.25b). This orientation was found toward the middle and tip of the dorsal fin of *Stenopterygius* where torsional stresses were probably greatest as again shown in the white shark (Lingham-Soliar 2005a, b). Also toward the anterior of the dorsal fin the fibers are predominantly in a single orientation, oriented at 50–60° to the long axis, in numerous layers before a reversal in orientation (again for several layers). This structural architecture of high fiber angles oriented at the same angle over numerous layers was considered to have functional implications connected with control surfaces dedicated to stiffness and stability during locomotion (Lingham-Soliar 2005a, b).

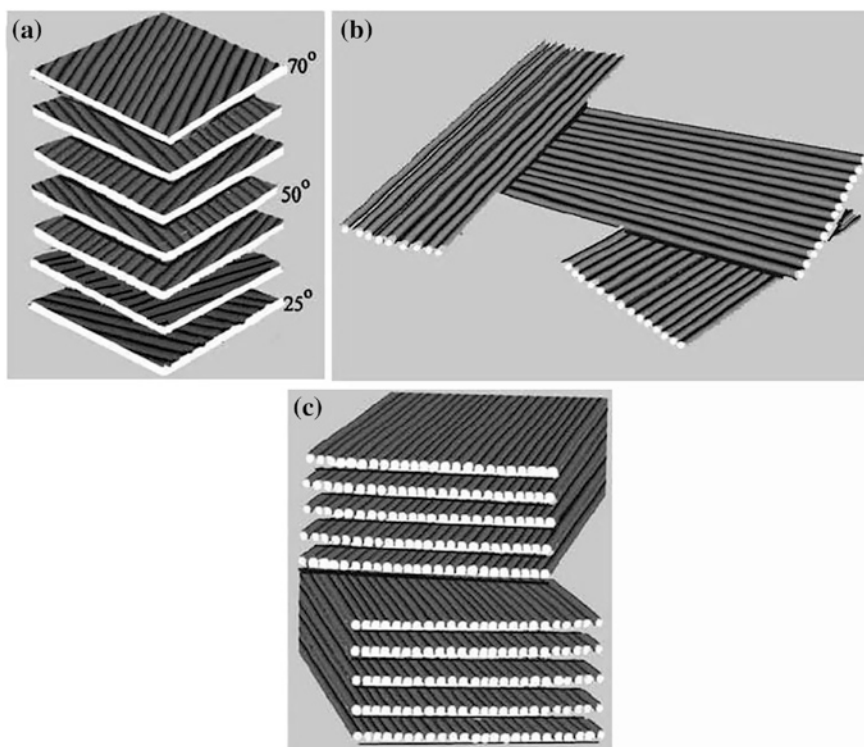
The dorsal lobe of the caudal fin also showed a number of areas with comparable fiber layers to those of the dorsal fin. However, despite more severe degradation in the caudal fin, two areas of preserved fibers in the dorsal lobe occur as rare transverse sections (cutting at near right angles to the fin's surface), allowing a high level of integumental information that is seldom seen in a fossil. The fibers were preserved helically wound around the upper caudal lobe, oppositely oriented at approximately +45° to the ichthyosaur's long axis. In the 3-D images from the unsupported dorsal lobe of the caudal fin, fibers follow the same orientation in about eight layers (right-handed) before a reversal (Fig. 2.25c) in orientation (left-handed). This is comparable to the anterior-midpoint of the dorsal fin and with the same functional implications, dedicated to stiffness and stability during locomotion (Lingham-Soliar 2005a, b).

A system of fibers with diagonal or bias arrangement of alternating left- and right-hand-oriented fibers at ~45° to the long axis of a structure such as a fin provides stiffness in shear that functions to reinforce the fin in the same way that that it does in fiber-reinforced thin cylinders (Lingham-Soliar 2005b; Clark and Cowey 1958; Wainwright et al. 1976). On the other hand, we find modifications of that system in living animals such as sharks and ichthyosaurs where external conditions may change and where fiber patterns may vary in different parts of the body or organ to deal with different or changing conditions and stresses. This allows a mechanical explanation for the fiber architecture at the base and tip of the dorsal fin where torsional stresses are probably greatest, and for the central part where bending stresses are greatest, as shown schematically in Fig. 2.26.

Findings of a highly organized cross-fiber architecture in the body and fins of thunniform ichthyosaurs such as *Ichthyosaurus* and *Stenopterygius* are important because it is now possible to tie them closely with respect to this crucial design strategy with that of the other three groups of extant thunniform swimmers.

We mentioned briefly in Volume 1 the need to resolve the physico-chemistry of the cross-fiber architecture in ichthyosaurs, which was more-or-less assumed to be collagenous. A little more detail is added here.

The triple helical structure of the amino acids plays a major role in the molecular conformation of collagen in living animals. This gives collagen a unique nano-physical structure or “fingerprint” ,i.e., the molecules of collagen types I, II, III, V, and XI are packed into D-periodic cross-striated fibrils (D-bands), typically D-67 nm, the characteristic axial periodicity of collagen, sometimes referred to as the quarter-stagger structure because adjacent molecules are transposed just

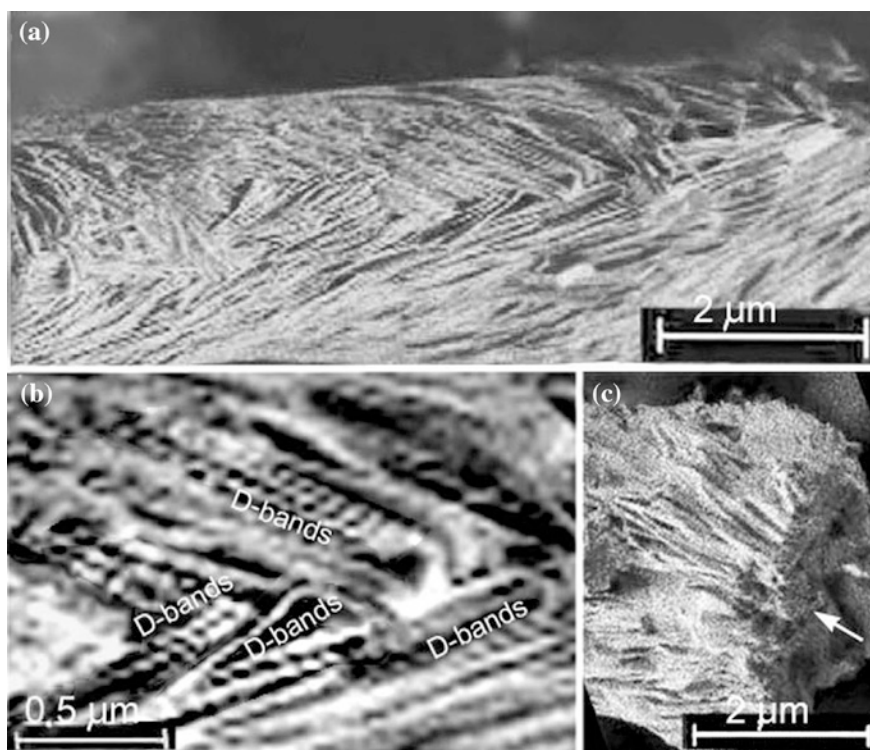


**Fig. 2.26** Schematic views of major fiber constructions in the control surfaces of *Stenopterygius*. Dorsal fin. **a** Exploded view of fibers in alternate layers of *left-* and *right-handed* orientations. Fiber angles differ from steep to shallow angles in the layers (range shown 25–70°). **b** At the base of the fin and at the tip, fiber layers show fibers oriented at low angles with the occasional layer with fibers at high angles. Caudal fin (*upper Lobe*). **c** Numerous layers with fibers oriented in the same direction before a reversal in direction

under one-quarter of their length in the axial direction (Smith 1968). However, this method requires valuable material for examination by SEM. Although I was understandably turned down in a request for a small sample of GLAHM V1180a for SEM analysis, the curator of the museum, Dr Neill Clark sent me some minute fragments that had come of the specimen during its relocating in the Hunterian Museum in Glasgow.

We were fortunately able to use the most advanced Zeiss electron microscope in South Africa at the time and fortuitously, two fibers of approximately 20–30  $\mu\text{m}$  length, with rounded cross sections of approximately 4  $\mu\text{m}$  in diameter (Fig. 2.27c) were identified ( $\sim 5,000$  magnification). However, it was at a much higher resolution ( $\sim 30,000$  times) that the most significant discovery was made (Lingham-Soliar and Wesley-Smith 2008). The SEM revealed numerous component fibrils (Fig. 2.27a, b) with the distinctive axial band periodicity of 66.12 nm (mean from numerous fibrils) consistent with the repeat D-band ultrastructure of type 1





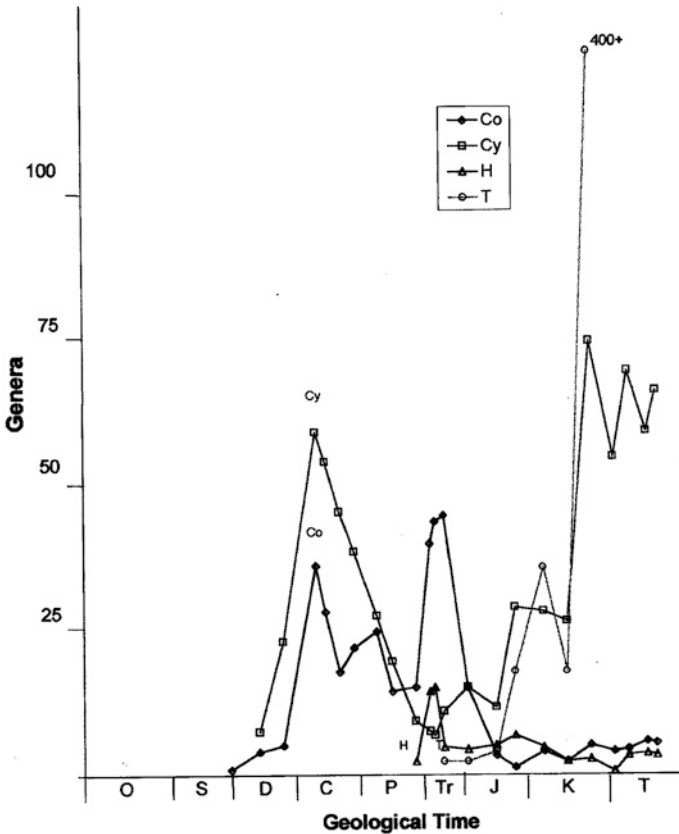
**Fig. 2.27** *Ichthyosaurus* (GLAHM V1180a). **a** Part of a 30  $\mu\text{m}$  long fiber packed with fibrils in remarkably good preservation. **b** Well-preserved D-bands or 67 nm repeat axial bands. **c** The sheared tip of a fiber. The fiber is eroded but shows an angled cross-sectional view. Fibers can be seen all the way to the fiber center. Lingham-Soliar and Wesley-Smith (2008), courtesy of the Royal Society of London

collagen (Smith 1968; Kadler et al. 1996; Reichlin et al. 2005). The findings demonstrated conclusively that the fibers preserved in the ichthyosaur integument were collagenous.

The question that remains is why did such a wonderfully advanced swimming animal such as the ichthyosaur not only become extinct but was among the first of the great marine reptiles (see Volume 1) to do so? It is a question I tried to answer a few years ago (Lingham-Soliar 2003).

During the early Jurassic monopoly of the swimming mode would have made them highly competitive as pursuit predators of fish and squid. As fast efficient predators they would have been secondary consumers in the food chain comparable to present day dolphins. So, why were ichthyosaurs the first of the four main groups of marine reptiles (the others being plesiosaurs, marine crocodiles, and mosasaurs) to go extinct toward the end of the Cretaceous? Ironically, extreme specialization as high-speed pursuit predators, as seen in some modern-day predators such as the cheetah, places a great strain on their feeding behavior particularly as

prey become more evasive, which in some animal groups may ultimately lead to extinction (Lingham-Soliar 2003). By the end of the Jurassic/early Cretaceous ichthyosaur monopoly of thunniform locomotion had come to an end. For instance the Late Jurassic saw the emergence of high-speed swimming fishes (if not thunniform, but fast) of the order Clupeiformes (herrings, anchovies, and allies) with a significant peak in the Lower Cretaceous and the greatest radiation of teleost fishes, which was so rapid that by the Upper Cretaceous 40 % of the families had appeared. The radiation of chondrichthian fishes paralleled that of the bony fishes and reached its greatest peak in the Upper Cretaceous. This invasion of fast-swimming fishes would have placed great energetic costs on ichthyosaurs, both as predators and prey, and may have played a significant part in ichthyosaur extinction (Lingham-Soliar 2003) (Fig. 2.28).



**Fig. 2.28** The rise of four major fish groups over time, condrichthyans (Cy), chondrosteans (Co), holosteans (H) and teleosteans (T). O Ordovician; S Silurian; D Devonian; C Carboniferous; P Permian; Tr Triassic; J Jurassic; K Cretaceous; T Tertiary. Graph from Lingham-Soliar (2003), redrawn from Thomson (1976), courtesy of Neues Jarbuch (abh)



On a lighter note, ichthyosaurs may well feel aggrieved that the thunniform swimming mode takes its name from *Thunnus* (tuna) given that Jurassic ichthyosaurs had evolved the swimming mode about 150 million years before tuna even came into existence (almost certainly a class A litigation). Yet if the name ichthyosauriform did take precedence, think of the added burden of having to say and spell it. One is reminded of Isabel Frances Bellous children's poem.

There once was an ichthyosaurus,  
Who lived when the earth was all porous,  
But he fainted with shame  
When he first heard his name,  
And departed a long time before us.

### 2.1.3 Anguilliform Swimmers

We have come full circle since discussing the eel, *Anguilla*, in Chap. 1, and now we briefly look at how the dermis might aid in the locomotion of the slowest of vertebrate swimmers discussed in this volume.

#### 2.1.3.1 Eel Dermis

Mary Hebrank (1980) notes the functions of fish skin are numerous, and are generally categorized as forms of protection from or adjustment to the environment and eel skin particularly performs these functions admirably. She mentions an interesting fact on a practical aspect of its toughness, in the service of humans—in Scandinavia it is used as door hinges. With its ability to produce copious quantities of mucus the skin can also assist the animal in adjusting to rather extreme environmental conditions—eels are not only euryhaline (capable of tolerating a wide range of salinity down to freshwater) but are also capable of aerial cutaneous respiration.

We saw above that sharks are constructed with the bulk of their musculature far anterior to its primary propulsive organ, the caudal fin, reaching an extreme in this evolutionary development in lamnid sharks. At the opposite end, the eel has its musculature distributed more evenly along its length, and uses nearly this whole length as its propulsive surface, lacking a distinct caudal fin (see Chap. 1; Fig. 2.1a).

While an external tendon might be of less benefit to an eel than it would be to a shark it should be kept in mind that both the eel and the shark (excluding Lamnid sharks) swim by undulatory propulsion, and in both cases the amplitude of the waves of bending increases as these waves travel backwards (Gray 1933). It is also interesting that in both Motta (1977) and Wainwright et al. (1978), the sharks studied were not thunniform but slower swimming sub-undulatory forms. Mary Hebrank's (1980) study was the first to investigate the anatomy of the dermal crossed-fiber

system since Wainwright et al.'s (1978) study and, in the archetypal undulatory swimmer. Thus, despite the morphological differences between sharks and eels, Hebrank (1980) wondered whether or not presence of a similar fiber system to that of sharks might contribute structural and mechanical properties to the locomotor behavior of eels.

Mary Hebrank showed through morphological examination and tensile tests that eel skin behaves very much as described in sharks including acting as an extensor. In addition, she pointed out that the eel exhibits another type of locomotor behavior in certain feeding situations. When the eel feeds on something which is too large to swallow, it bites into the food and then rotates about its own long axis several times, with great speed, in order to tear off the mouthful. This motion can sometimes be seen when an eel is caught on a hook and line, and it has been witnessed in eels in aquaria. When this “corkscrew” motion occurs, the eel’s skin must be stressed in torsion. As we know, a cylinder wrapped with inextensible fibers resists torsion most rigidly when the fibers are wound at an angle of  $45^\circ$  with the long axis (the direction of maximum tensile stress during torsion). Thus, when the eel performs its corkscrew motion, the collagen fibers of one helical set (either the right- or left-helical set, depending on the direction of the motion) are being pulled along their long axes. Since the fibers behave as though they are continuous, the tensile force is transmitted along the length of the fish. In this way it is possible that the eel need only generate a twisting moment about the head in order to rotate the whole body. It appears that a fiber angle of  $45^\circ$  is uniquely suited to this corkscrew motion.

Once we discovered that the invertebrate threshold for the crossed-fiber architecture had crossed over to vertebrates it now seems no surprise that the cross-fiber helically wound fiber structure can be regarded as a biomechanical design principle in many animals (and plants) and materials perhaps comparable in importance to, e.g., other design principles such as beams and thin-walled cylinders and indeed frequently a part of them. In vertebrates its chemistry has been restricted to collagen, unlike in invertebrates where, e.g., it includes collagen and chitin, and in plants, cellulose (Gibson 2012). However, the story does not end there. We will see in Chap. 5 the latest group of animals to join this structural design club, birds, and with them a new material to incorporate the design in vertebrates,  $\beta$ -keratin.

## References

- Alexander RMcN (1965) The lift produced by the heterocercal tail of Selachii. *J Exp Biol* 43:131–138
- Alexander RMcN (1987) Bending of cylindrical animals with helical fibers in their skin or cuticle. *J Theor Biol* 124:97–110
- Alexander R McN (1988) Elastic mechanisms in animal movement. Cambridge University Press, Cambridge
- Bass AJ, Ballard JA (1972) Buoyancy control in the shark *Odontaspis taurus* (Rafinesque). *Copeia* 1972:594–595
- Blake RW (1983) Fish locomotion. Cambridge University Press, Cambridge

- Boustany AM, Davis SF, Pyle P, Anderson SD, Le Boeuf BJ, Block B (2002) Expanded niche for white sharks. *Nature* 415:35–36
- Clark RB (1964) Dynamics of metazoan evolution. Clarendon Press, Oxford
- Clark RB, Cowey JB (1958) Factors controlling the change of shape of certain nemertean and turbellarian worms. *J Exp Biol* 35:731–748
- Cliff G, Dudley SFJ, Jury MR (1996) Catches of white sharks in KwaZulu-Natal, South Africa and environmental influences. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, pp 351–362
- Dawson MA, Gibson LJ (2006) Biomimetics: extending nature's design of thin wall shells with cellular cores. Press WIT transactions on ecology and the environment, vol 87. WIT, Southampton
- Delair JB (1966) Unusual preservation of fibrous elements in an ichthyosaur skull. *Nature* 212:575–576
- Donley JM, Dickson KA (2000) Swimming kinematics of juvenile kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). *J Exp Biol* 203:3103–3116
- Donley JM, Sepulveda CA, Konstantinidis P, Gemballa S, Shadwick RE (2004) *Nature* 429:61–65
- Drucker EG, Lauder GV (2001) Locomotor function of the dorsal fin in teleost fishes: experimental analysis of wake forces in sunfish. *J Exp Biol* 204:2943–2958
- Ferry LA, Lauder GV (1996) Heterocercal tail function in leopard sharks: a three-dimensional kinematic analysis of two models. *J Exp Biol* 199:2253–2268
- Fierstine HL, Walters V (1968) Studies in locomotion and anatomy of scombrid fishes. *Mem South Calif Acad Sci* 6:1–31
- Fish FE, Shannahan LD (2000) The role of the pectoral fins in the body trim of sharks. *J Fish Biol* 56:1062–1073
- Fish FE, Peacock JE, Rohr JJ (2003) Stabilization mechanism in swimming odontocete cetaceans by phased movements. *Mar Mamm Sci* 19:515–528
- Frazzetta TH (1988) The mechanics of cutting and the form of shark teeth (*Chondrichthyes*, *Elasmobranchii*). *Zoomorphology* 108:93–107
- Frazzetta TH (1994) Feeding mechanisms in sharks and other elasmobranchs. *Adv Comp Environ Physiol* 18:31–57
- Frazzetta TH, Prange CD (1987) Movements of cephalic components during feeding in some requiem sharks *Carcharhiniformes*: (*Carcharhinidae*). *Copeia* 1987:979–993
- Froese R, Pauly D (2002) Fishbase. Web publication. [www.fishbase.org](http://www.fishbase.org) (13 October 2002)
- Gans C, Parson T (1964) A photographic atlas of shark anatomy. University of Chicago Press, Chicago
- Gibson LJ (2012) The hierarchical structure and mechanics of plant materials. *J R Soc Interface* 9:1–18. doi:[10.1098/rsif.2012.0341](https://doi.org/10.1098/rsif.2012.0341)
- Gill-King H (1997) Chemical and ultrastructural aspects of decomposition. In: Haglund WD, Sorg MH (eds) Forensic taphonomy: the postmortem fate of human remains. CRC Press, Boca Raton, pp 547–549
- Graham JB, Dewar H, Lai NC, Lowell WR, Arce SM (1990) Aspects of shark swimming performance determined using a large water tunnel. *J Exp Biol* 151:175–192
- Gray T (1933) Studies in animal locomotion. I. The movement of fish with special reference to the eel. *J Exp Biol* 10:88–104
- Hebrank MR (1980) Mechanical properties and locomotor functions of eel skin. *Biol Bull* 158:58–68
- Hebrank MR, Hebrank JH (1986) The mechanics of fish skin: lack of an 'external tendon' role in two teleosts. *Biol Bull* 171:236–247
- Heithaus MR, Dill LM (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83:480–491
- Heithaus MR, Marshall DJ, Buhleier BM, Dill LM (2001) Employing crittercam to study habitat use and behavior of large sharks. *Mar Ecol Prog Ser* 209:307–310
- Katz S, Jordon C (1997) A case for building integrated models of aquatic locomotion that couple internal and external forces. In: Proceedings of the 10th International Symposium

- Kadler KE, Holmes DF, Trotter JA, Chapman JA (1996) Collagen fibril formation. *Biochem J* 316:1–11
- Lauder GV (2000) Function of the caudal fin during locomotion in fishes: kinematics, flow visualization and evolutionary patterns. *Am Zool* 40:101–122
- Lighthill J (1975) Mathematical biofluid dynamics. Soc Ind Appl Math (Philadelphia)
- Lingham-Soliar T (1999) Rare soft tissue preservation showing fibrous structures in an *ichthyosaurus* from the Lower Lias (Jurassic) of England. *Proc R Soc Lond B* 266:2367–2373
- Lingham-Soliar T (2001) The ichthyosaur integument: skin fibers, a means for a strong, flexible and smooth skin. *Lethaia* 34:287–302
- Lingham-Soliar T (2003) Extinction of ichthyosaurs: a catastrophic or evolutionary paradigm? *NJb Geol Paläont Abh* 228:421–452
- Lingham-Soliar T (2005a) Dorsal fin in the white shark, *Carcharodon carcharias*: a dynamic stabilizer for fast swimming. *J Morphol* 263:1–11
- Lingham-Soliar T (2005b) Caudal fin in the white shark, *Carcharodon carcharias* (Lamnidae): a dynamic propeller for fast, efficient swimming. *J Morphol* 264:233–252. doi:[10.1002/jmor.10328](https://doi.org/10.1002/jmor.10328)
- Lingham-Soliar T, Reif W-E (1998) Taphonomic evidence for fast tuna-like swimming in Jurassic and Cretaceous ichthyosaurs. *N Jb Abh* 207:171–183
- Lingham-Soliar T, Plodowski G (2007) Taphonomic evidence for high-speed adapted fins in thunniform ichthyosaurs. *Naturwissenschaften* 94:65–70
- Lingham-Soliar T, Wesley-Smith J (2008) First investigation of the collagen D-band ultrastructure in fossilized vertebrate integument. *Proc R Soc Lond B* 275:2207–2212. doi:[10.1098/rspb.2008.0489](https://doi.org/10.1098/rspb.2008.0489)
- Long JH Jr, Pabst DA, Shepherd WR, McLellan WA (1997) Locomotor design of dolphin vertebral columns: Bending mechanics and morphology in *Delphinus delphis*. *J Exp Biol* 200:65–81
- Mann RW, Bass WM, Meadows L (1990) Time since death and decomposition of the human body: 544 variables and observations in case and experimental field studies. *J Forensic Sci* 35:103–111
- McGowan CA (1999) A practical guide to vertebrate mechanics. Cambridge University Press, Cambridge
- Micozzi M (1986) Experimental study of postmortem change under field conditions: effects of freezing, 550 thawing and mechanical injury. *J Forensic Sci* 31:953–961
- Moin P, Bewley T (1994) Feedback control of turbulence. *Appl Mech Rev* (part 2) 47:3–13
- Moin P, Kim J (1997) Tackling turbulence with supercomputers. *Am Sci* 276(1):46–52
- Moss SA (1972) The feeding mechanism of sharks of the family Carcharinidae. *J Zool Lond* 167:123–136
- Motta PJ (1977) Anatomy and functional morphology of dermal collagen fibers in sharks. *Copeia* 1977:454–464
- Motta P, Habegger ML, Lang A, Hueter R, Davis J (2012) Scale morphology and flexibility in the shortfin mako *Isurus oxyrinchus* and the blacktip shark *Carcharhinus limbatus*. *J Morphol*. doi:[10.1002/jmor.20047](https://doi.org/10.1002/jmor.20047)
- Nareish MD, Arumugam V, Sanjeevi R (1997) Mechanical behaviour of shark skin. *J Biosci* 22:431–437
- Nauen JC, Lauder GV (2002) Hydrodynamics of caudal fin locomotion by chub mackerel, *Scomber japonicus* (Scombridae). *J Exp Biol* 205:1709–1724
- Pabst DA (1990) Axial muscles and connective tissues of the bottlenose dolphin. In: Leatherwood S, Reeves RR (eds) the bottlenose dolphin. Academic Press, San Diego, pp 51–67
- Pabst DA (1996a) Morphology of the subdermal connective sheath of dolphins: a new fiber-wound, thin-walled, pressurized cylinder model for swimming vertebrates. *J Zool Lond* 238:35–52
- Pabst DA (1996b) Springs in swimming animals. *Am Zool* 36:723–735

- Pabst DA (2000) To bend a dolphin: convergence of force transmission designs in cetaceans and scombrid fishes. *Am Zool* 40:146–155
- Randall JE (1983) Size of the great white shark (*Carcharodon*). *Science* 181:169–170
- Reichlin T, Wild A, Dürrenberger M, Daniels AU, Aebi U, Hunziker PR, Stolz M (2005) Investigating native coronary artery endothelium in situ and in cell culture by scanning force microscopy. *J Struct Biol* 152:52–63. doi:[10.1016/j.jsb.2005.07.009](https://doi.org/10.1016/j.jsb.2005.07.009)
- Reif W-E, Weishampel D (1986) Anatomy and mechanics of the lunate tail in lamnid sharks. *Zool Jb Anat* 114:221–234
- Shadwick RE (2005) How tunas and lamnid sharks Swim: an evolutionary convergence. *Am Sci* 93:524–531
- Smith JW (1968) Molecular pattern in native collagen. *Nature* 219:157. doi:[10.1038/219157a0](https://doi.org/10.1038/219157a0)
- Springer S (1961) Dynamics of the feeding mechanism of large galeoid sharks. *Am Zool* 1:185–193
- Thomson KS (1976) On the heterocercal tail in sharks. *Paleobiology* 2:19–38
- Thomson KS, Simanek DE (1977) Body form and locomotion in sharks. *Am Zool* 17:343–354
- Tordonato DS (2003) The effects of freezing on the mechanical properties of articular cartilage. Thesis submitted to the Faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of Master of Science in Mechanical Engineering. Blacksburg, Virginia
- Tricas TC, McCosker JE (1984) Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proc Calif Acad Sci* 43:221–238
- Tricas TC, Taylor LR, Naftel G (1981) Diel behavior of the tiger shark, *Galeocerdo cuvier*, at French Frigate Shoals, Hawaiian Islands. *Copeia* 1981:904–908
- Van Ee CA, Chasse AL, Myers BS (1998) The effect of postmortem time and freezer storage on the mechanical properties of skeletal muscle. Stapp Car Crash Conference
- Wainwright SA, Biggs WD, Currey JD, Gosline JM (1976) Mechanical design in organisms. Edward Arnold, London
- Wainwright SA, Vosburgh F, Hebrank JH (1978) Shark skin: function in locomotion. *Science* 202:747–749
- Webb PW (1983) Speed, acceleration and maneuverability of two teleost fishes. *J Exp Biol* 102:115–122
- Webb PW (1984) Form and function in fish swimming. *Sci Am* 251:58–68
- Webb PW, Weihs D (1983) Optimization of locomotion. In: Webb P, Weihs D (eds) *Fish biomechanics*. Praeger, New York, pp 339–371
- Westneat MW, Hoesle W, Pell CA, Wainwright SA (1993) The horizontal septum: mechanics of force transfer in locomotion of scombrid fishes (Scombridae, Perciformes). *J Morph* 217:183–204
- Wilga CD, Lauder GV (2002) Function of the heterocercal tail in sharks: quantitative wake dynamics during steady horizontal swimming and vertical maneuvering. *J Exp Biol* 205:2365–2374
- Wilga CD, Lauder GV (2004) Hydrodynamic function of the shark's tail. *Nature* 430:850
- Woo S, Orlando J, Camp J, Akeson W (1986) Effects of postmortem storage by freezing on ligament tensile behaviour. *J Biomech* 19:399–404

The Vertebrate Integument Volume 2

Structure, Design and Function

Lingham-Soliar, T.

2015, XIII, 348 p. 208 illus., 42 illus. in color., Hardcover

ISBN: 978-3-662-46004-7