



SYMPOSIUM

Convergence in Thunniform Anatomy in Lamnid Sharks and Jurassic Ichthyosaurs

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Synopsis Among extinct ichthyosaurs the Jurassic forms *Ichthyosaurus* and *Stenopterygius* share a number of anatomical specializations with lamnid sharks, characterized in the white shark, *Carcharodon carcharias*. These features allow their inclusion within the mode of high-speed thunniform swimming to which only two other equally distinctive phylogenetic groups belong, tuna and dolphins—a striking testament to evolutionary convergence. Jurassic ichthyosaurs evolved from reptiles that had returned to the sea (secondarily adapted) about 250 million years ago (MYA) while lamnid sharks evolved about 50 MYA from early cartilaginous fishes (originating ca. 400 MYA). Their shared independently evolved anatomical characteristics are discussed. These include a deep tear-drop body shape that helped initially define members as thunniform swimmers. Later, other critical structural characteristics were discovered such as the crossed-fiber architecture of the skin, high-speed adapted dorsal and caudal fins, a caudal peduncle and series of ligaments to enable transmission of power from the musculature located anteriorly to the caudal fin. Both groups also share a similar chemistry of the dermal fibers, i.e., the scleroprotein collagen.

Introduction

Modern fishes comprise the largest and most successful group of all vertebrates on earth. The higher fishes are divided into two major groupings, Chondrichthyes or cartilaginous fishes and Osteichthyes or bony fishes. Their origins are ancient, arising sometime in the Devonian (Helfman et al. 2009). The extraordinary rise is noted among, e.g., the cartilaginous fishes, which includes skates, chimaeras, rays, and sharks, the latter of particular interest here. The first true shark-like fossils of elasmobranchs occur in the early Devonian. One of the first sharks was *Cladoseleche*, which had a typical shark-like, elongated body shape, and a large heterocercal tail. The structural pattern of *Cladoseleche*, while primitive for most sharks, is important because it shows the bauplan from which modern sharks would develop and would lay the foundations for their extraordinary success (Romer 1971). This would include, among other things, important anatomical and biomechanical developments, including

a streamlined body form with strategic locations of the dorsal, pectoral, and pelvic fins and a large caudal fin as propeller (Helfman et al. 2009).

About 50 million years ago a more heavy deep-bodied, streamlined form of shark with a crescent shaped tail evolved giving rise to a few species in the family Lamnidae or Isuridae, including the white shark, *C. carcharias* (Lingham-Soliar 2005a, 2005b; Figure 1A), the mako, *Isurus oxyrinchus* (Donley et al. 2004), and the salmon shark, *Lamna nasus* (Helfman et al. 2009). They are among the most active apex predators cruising the world's oceans. Their swimming style changed from the carangiform mode to the highly evolved thunniform (Figure 2A and B), which they share with just two other extant groups of marine vertebrates, tuna (from which the name is derived) and dolphins. It is worth mentioning that there is a thin line between the swimming mode of these groups and of certain other fast swimmers e.g., the billfishes and marlins (Istiophoridae) and swordfish (Xiphiidae), generally

referred to as carangiforms (Lindsey 1978; Braun and Reif 1985) but considered thunniform by Blake (1983). More work is clearly needed on these extraordinary fishes, especially with respect to their swimming mode.

In the thunniform animal, the two most obvious characteristics are the deep streamlined body (high fineness ratio, i.e., the ratio of the length of a body to its maximum width) and the crescent or lunate shaped tail (Figs. 1 and 2). During swimming this body form, aided by a stiff caudal peduncle, reduces lateral deflection (and drag) and confines forward propulsion to the fanning motions or oscillations of the lunate caudal fin (Lindsey 1978). The lunate caudal fin of a thunniform swimmer looks like an aerofoil and it generates lift the same way as an aeroplane wing does. Lift is created perpendicular to the direction of fluid flow around the aerofoil shape, so in the thunniform swimmer, the force produces forward thrust instead of upward lift. The fin is oriented at a less oblique angle than the path the fin follows, and this difference is called alpha (α), the angle of attack. The result is asymmetrical water flow over the fin, with less pressure at the rear-facing surface than the forward-facing surface, producing a forward lift force (McGowan 1999; Sfakiotakis et al. 1999; Shadwick 2005).

Lighthill (1975), however, was the first to notice striking parallels between the extinct Jurassic ichthyosaurs and living members of thunniform swimmers. Despite the phylogenetically distinctive histories of tuna, dolphins, lamnid sharks, and ichthyosaurs they all share a close similarity of body and tail fin shape, a case of evolutionary convergence in response to similar physical forces in the environment. Ichthyosaurs were members of an extinct group of marine reptiles that had their origins on land, hence they are referred to as secondarily adapted to water. They had a wide geographic distribution and they spanned almost the entire Mesozoic Era. Perhaps no other group of extinct marine reptiles has captured the imagination of the public more than the ichthyosaurs, which are represented by a variety of forms (McGowan 1973, 1992a, 1993; Motani 1999, 2000) with lengths ranging from about 1 to 15 m while one gigantic species, *Shastasaurus sikanniensis*, was 21 m long (Nicholls and Manabe 2004). It was in the Jurassic, however, that ichthyosaurs achieved their classic fish-like body shape, giving rise to their name (literally “fish-lizards” from Greek *ichthys* “fish” and *sauros* “lizard”). They possessed a long, toothed jaw, and large eyes (Fig. 1B). Yet, part of their great fascination was that ichthyosaurs also look strikingly like

dolphins. Also remarkable is the fact that Jurassic ichthyosaurs despite being descended from egg-laying reptilian ancestors are believed to have produced young via live birth. Several specimens found in the excellent fine-grained early Jurassic shale of southern Germany, particularly around Holzmaden, show numerous embryos within the body outline and some apparently in the process of giving birth (Carroll 1988).

Although ichthyosaurs studies have been important in a variety of biological and paleontological contexts, e.g., taxonomy, evolutionary history, discoveries, controversies (Martill 1987, 1993; Wild 1990) and early interpretations of soft-tissue material (Broili 1942; Wiman 1946; Delair 1966), these have been well documented. However, one question is worth briefly mentioning, namely the authenticity of the soft tissue preservations through diagenetic mineralization (Allison 1988). Recently, Smith et al. (2015) alleged that protein does not preserve as fossils while earlier allegations were that the soft tissue preservations were either carbonaceous outlines or bacterial mats (Martill 1987). Martill subsequently stated that the caudal fins and tails that he had originally questioned were genuine, following which he (Martill 1995) described muscle tissue in a Sinemurian ichthyosaur from southern UK. On the alleged inability of skin to preserve, Lindgren et al. (2011) described a mosasaur with preserved skin and fibers, which they compared with those described in ichthyosaurs (Lingham-Soliar 1999, 2001) and in a number of living marine vertebrates, e.g., dolphins, tuna, and sharks. Lindgren et al. (2014) also described fossilized skin of an ichthyosaur, YORYM 1993.338, in which melanosomes, the color granules associated with skin and feather color, were identified amidst dark traces of the skin. It is noteworthy that in vertebrates collagen comprises about 40% of the total protein (about 33% in humans). Therefore, to cap just these few identifications of skin preservation among the many known, collagen was identified in skin fibers in the ichthyosaur, *Ichthyosaurus*, by its molecular “fingerprint” the D-band ultrastructure (Lingham-Soliar and Wesley-Smith 2008), which will be discussed further below.

The present study highlights the strong convergence between lamnid sharks and the Jurassic ichthyosaurs with particular respect to their high-speed form of locomotion. I pay particular attention to parallels in the complex anatomical structures involved in thunniform locomotion in these two group of animals. These include discoveries in recent years in sharks, tuna, and dolphins of certain other vital morphological structures besides body and tail shape that are also essential for

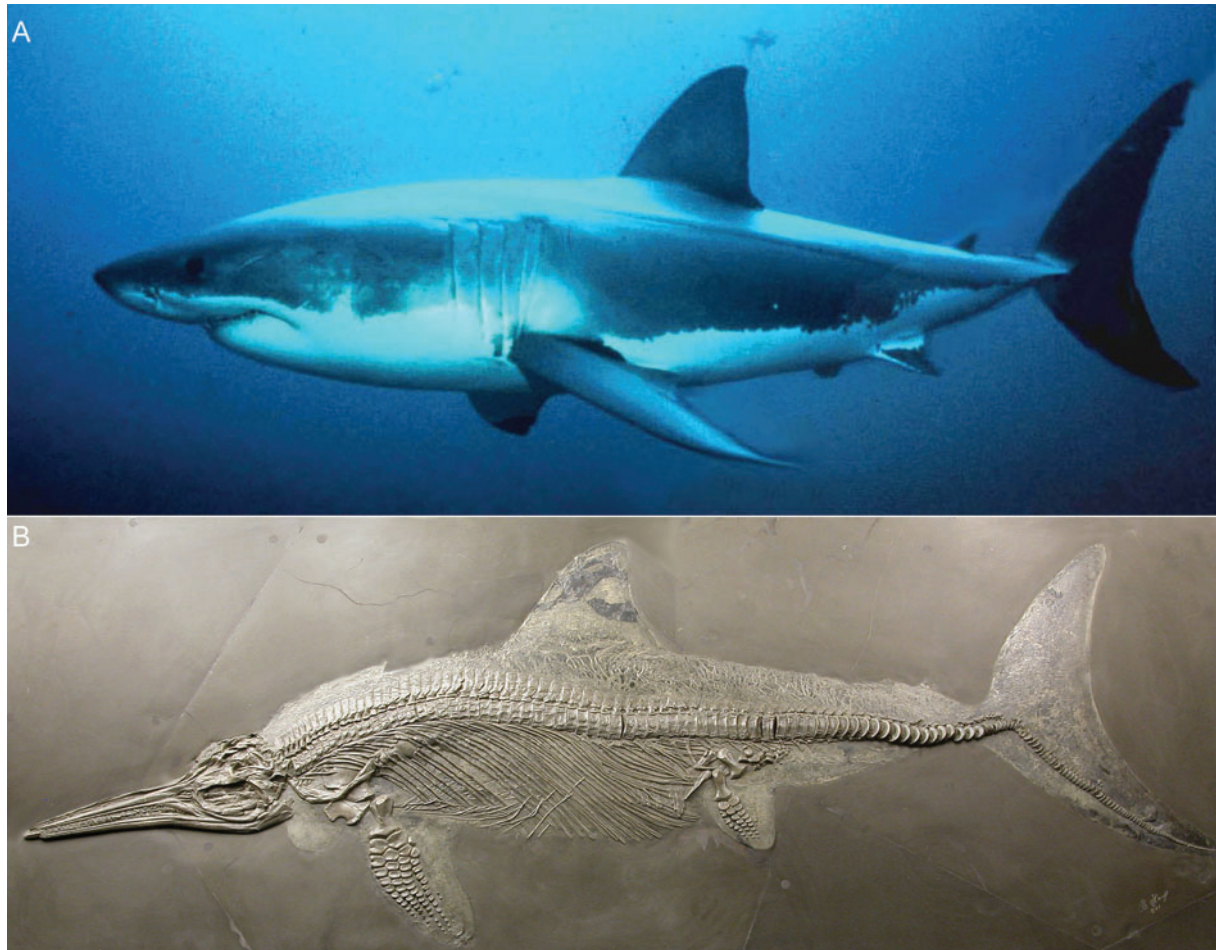


Fig. 1 Two thunniform swimmers showing the deep, torpedo-shaped body and large dorsal fin and high-aspect-ratio caudal fin. **(A)** The white shark, *Carcharodon carcharias* (after Lingham-Soliar 2005b). **(B)** The ichthyosaur, *Stenopterygius quadricissus* SMF 457 (Senckenberg Museum, Germany), approximately 2.3 m long (after Lingham-Soliar and Plodowski 2007).

thunniform swimming principally a crossed-fiber structure of the dermis (comprising the virtually inelastic fiber, collagen; Lingham-Soliar and Wesley-Smith 2008), high-speed adapted dorsal and caudal fins, a caudal peduncle, and series of ligaments to enable transmission of power from the musculature located anteriorly to the caudal fin. Using this new information it was now possible to look at the concept of thunniform swimming in the Jurassic ichthyosaurs *Ichthyosaurus* and *Stenopterygius* with a fresh perspective. Of the four taxonomic groups, I considered these conditions to have been most closely shared with lamnid sharks. While other members of the family Lamnidae, *I. oxyrinchus* and *L. nasus*, almost undoubtedly had a crossed-fiber architecture of the body and control structures, *C. carcharias* is chosen to represent the family because most of the related work was performed on this species (Lingham-Soliar 2005a, 2005b). It is important to bear in mind too, that many sharks beside members of the Lamnidae have a cross-fiber architecture of the skin

(Motta 1977), with a similar function that aids bending (see below). However, the development is considered to be greatest in lamnids, at both the microstructural and gross structural levels, as described in the architecture of the skin and of the dorsal and caudal fins respectively (Lingham-Soliar 2005a, 2005b). The lamnid sharks are strikingly different from the non-lamnoid sharks in these and many other characteristics and unlike the latter (McGowan 1992a) are an appropriate analog for the Jurassic ichthyosaurs.

The crossed-fiber architecture of the dermis

The body

The crossed fiber dermal architecture and its biomechanical implications were first described in a classic study on the skin of nematode worms, which exquisitely combined biology and mathematics (Clark and Cowey 1958). The model they described shows the worm as a fluid-filled, pressurized tube stiffened by helical wrappings of

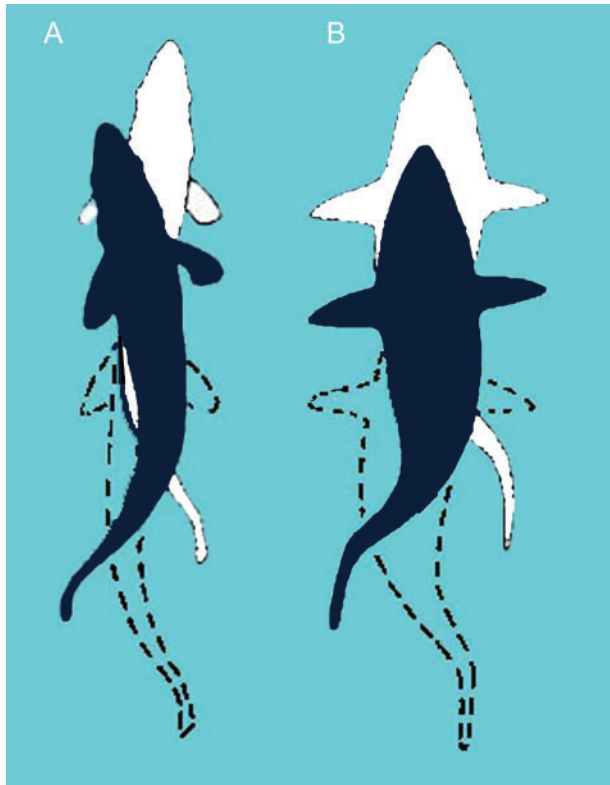


Fig. 2 Two swimming modes. (A) Carangiform mode used by many fishes. (B) Highly specialized thunniform mode used by just four groups of vertebrates (modified from Lindsey 1978).

inextensible fibers wherein 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

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

This shows that V decreases toward zero as θ goes to 0° (a long, thin thread) or 90° (a flat disc), and it peaks at an intermediate angle of 54.74° .

Motta (1977), however, was the first to show a crossed-fiber architecture in the dermis of a vertebrate, in the non-lamnid sharks. Although the function of these fibers in a large vertebrate was unclear at the time, Motta (1977) touched upon a critical answer, which was subsequently followed up by Wainwright et al. (1978). These workers were able to show that the fiber architecture in the lemon shark (non-lamnid), *Negaprion brevirostris*, with increasing hydrostatic pressure during swimming, conformed to areas of greatest stress, as in a thin, fiber-reinforced cylinder (and in nematode worms), namely, along the hoop of the animal (Wainwright et al. 1978). Note, stress along the hoop of a pressurized cylinder is twice that along the longitudinal

axis, which explains why, e.g., when sausages swell during frying they split along their length. In engineering as well as in nature a solution is to reinforce the hoop with fibers aligned at 55° (or near enough) to the long axis.

This system of fibers also plays a vital role in enabling the animal to bend its body while still maintaining stiffness. This is best understood if one considers the shark's skin as a cloth cut on the diagonal or bias. The normal square cut cloth consists of fibers that run vertically and horizontally (warp and weft). Pulling along either of these, the cloth will extend very little (i.e., it is stiff in tension). However pulling along the bias of the cloth (opposite diagonal points) allows it to extend greatly (Gordon 1978). Similarly, with shark skin, fibers aligned along the bias allow the skin to extend as required during bending of the tail. This action concomitantly stresses the fibers aligned at 45° to the shark's long axis and increases stiffness around the hoop or circumference of the animal. Similar findings of a crossed-fiber system were subsequently found in the skin of tuna (Hebrank and Hebrank 1986), dolphins (Pabst 1996), and a lamnid shark represented by *Carcharodon carcharias* (Lingham-Soliar 2005a, 2005b) (Fig. 3A-C), and also noted here in *Isurus oxyrinchus* (Figure 3D), with function similarly interpreted.

With this wealth of new information in extant thunniform swimmers there was the potential to reevaluate the fiber architecture in the dermis of Jurassic ichthyosaurs in an attempt to test their place among the other members. Suffice it to say, a major problem was to find the rare soft-tissue specimens necessary for the study. Note, this was not simply soft tissue or even fibers, known to some small extent in the literature, but specifically fibers that could reasonably be interpreted as belonging to a cross-fibered pattern. It would involve examination of scores of specimens. Two species of Jurassic ichthyosaurs, *Ichthyosaurus* from the Lower Lias of Gloucestershire and *Stenopterygius quadriscissus* from the Posidonia Shales of southern Germany were found to have areas with significant soft tissue preservation. The preservational conditions were also very different, *Ichthyosaurus* is preserved in a clay nodule and *Stenopterygius* in shale, giving added support to the findings (Lingham-Soliar 2001).

Remarkably, three size classes of the crossed fiber filaments were identified in different levels of the integument over virtually the entire surface of the body of *Stenopterygius* (Figure 4A, B, C), including in the head of *Ichthyosaurus* (Figure 4D) (Lingham-

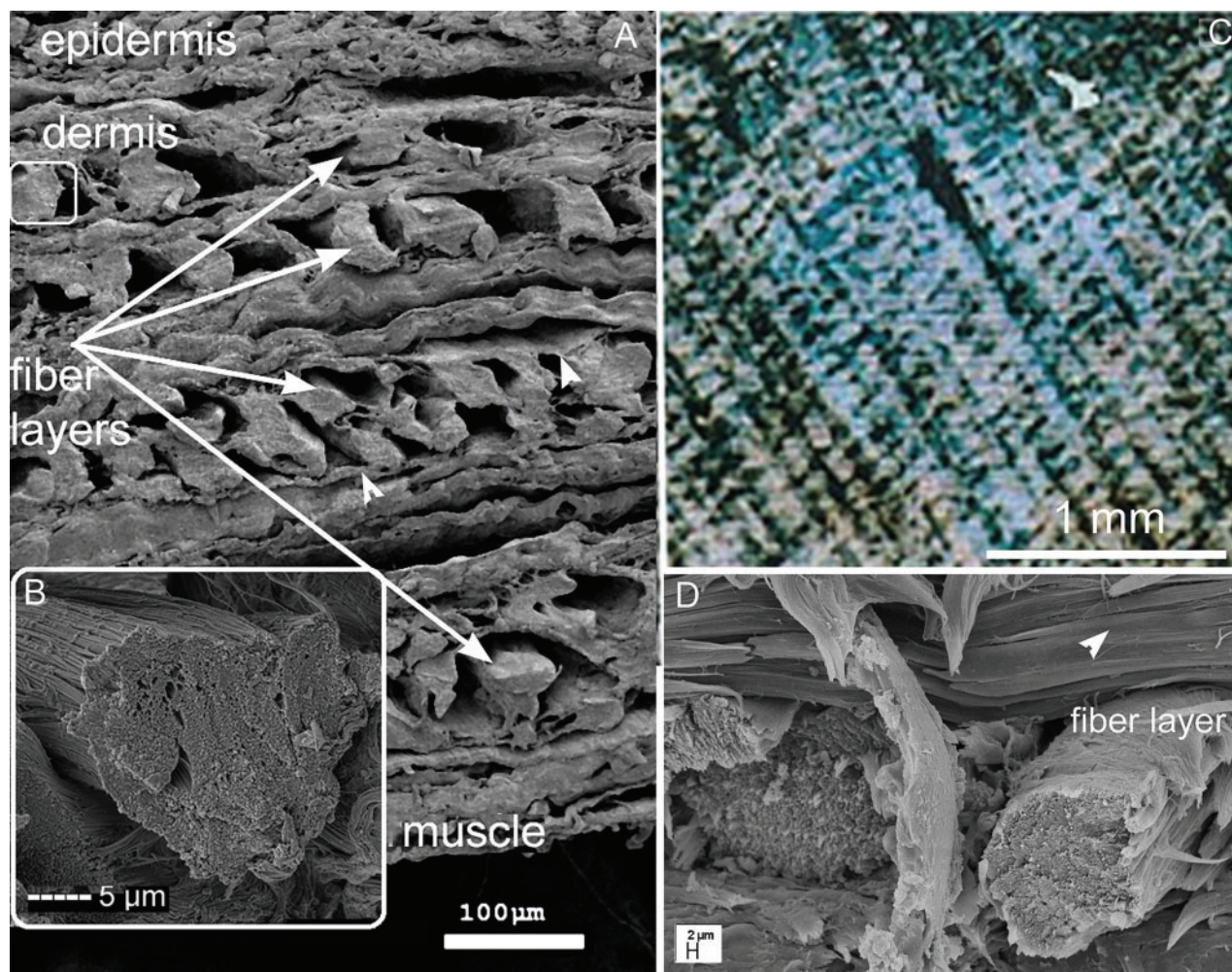


Fig. 3 Dermal fibers in the body. *Carcharodon carcharias* (A–C). (A) SEM of a cross-section taken just anterior to the caudal peduncle. (B) Inset, detail of fiber bundle demarcated above. (C) Histological sagittal section taken from caudal peduncles in which fibers are about 10–15% steeper than in the rest of the body (arrow shows body long axis). (D) SEM of similar fiber bundles in the body of *Isurus oxyrinchus*. Arrowheads mark connective tissues that permit smooth movements of the fibers.

Soliar 1999, 2001). The angles of these fibers were found to vary between 25° and 75° to the longitudinal axis of the animals, depending on their location in the body. As found in sharks, this coincides with different amounts of stress in different regions of the body (Naresh et al. 1997).

In *Stenopterygius* the thickest fibers were described located deepest in the skin and the thinnest in the outermost layers (Lingham-Soliar 2001) (Figure 4A, B). Yet, a hierarchical system of fibers was not known in the extant thunniform swimmers, tuna, and dolphins, nor in non-lamnoid sharks, the only sharks investigated at the time in this context (Motta 1977). However, a hierarchical fiber architecture of the dermis would receive definitive support a few years later when it was discovered in the dermis of *C. carcharias* (Lingham-Soliar 2005b), emphasizing the robustness of the ichthyosaur findings.

Functionally it seemed that the strongest fiber movements occurred deepest in the dermis (Lingham-Soliar 2005b). This distinctive evolutionary development of the cross-fiber hierarchy in *C. carcharias*, as opposed to that of smaller non-lamnoid sharks (Motta 1977), and in *Stenopterygius* was interpreted as a characteristic closely tied to the thunniform mode of locomotion (Lingham-Soliar 2005b). It is yet to be investigated in tuna and dolphins. In addition to body and tail shape, it was another important criterion for defining the fast thunniform mode of locomotion in lamnoid sharks and Jurassic ichthyosaurs (Lingham-Soliar 1999, 2001).

Control structures

The dorsal fin

Thrust in thunniform swimmers is largely restricted to the caudal oscillating hydrofoil, which minimizes

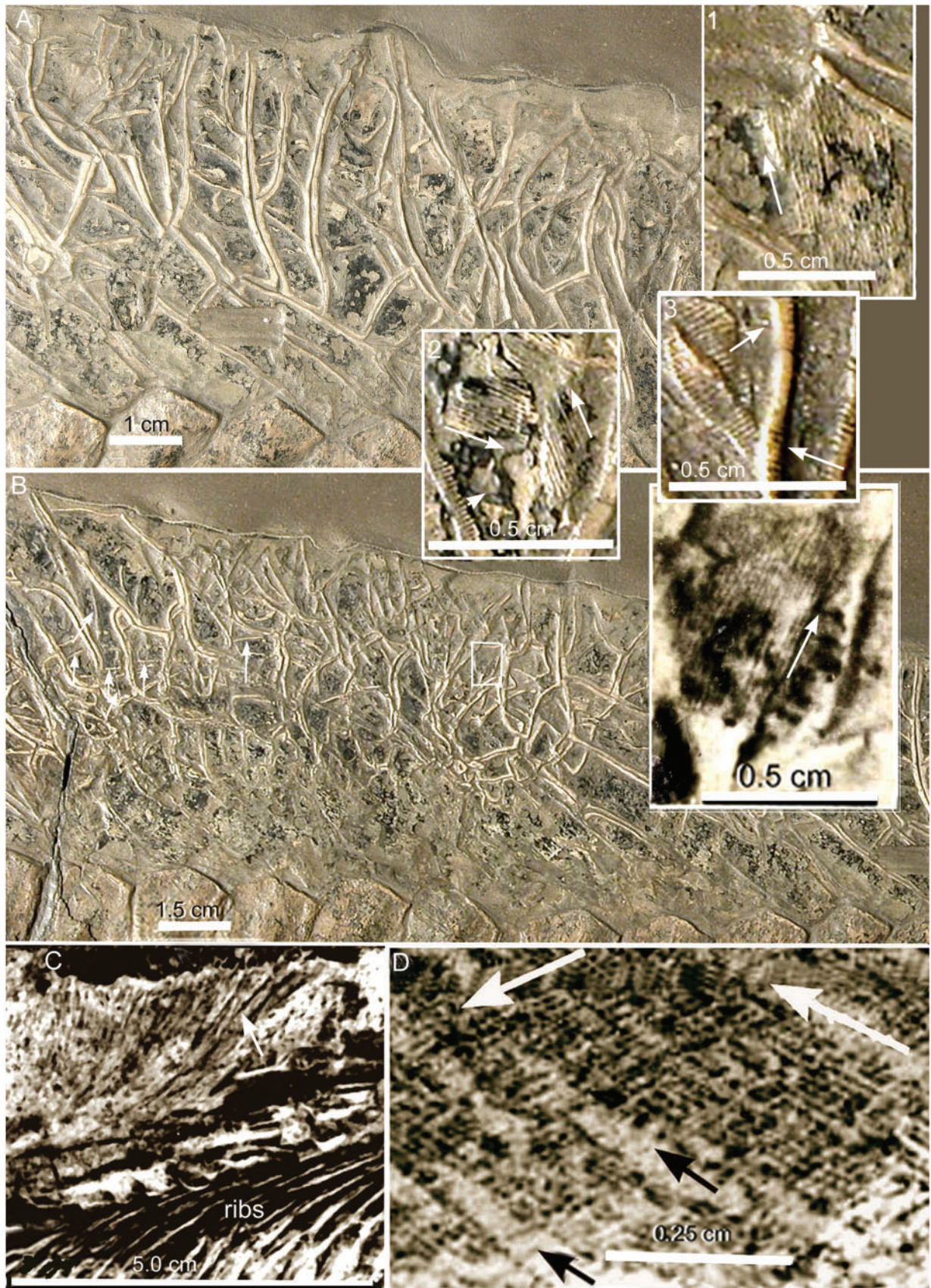


Fig. 4 Ichthyosaur dermal fibers over the body. *Stenopterygius*. (A) (B) Class 1 (thickest) dermal fibers disorganized during preservation (cf. (C)). Among the class 1 fibers are traces of class 2 and class 3 fibers including layers showing opposite orientations as well as some

body drag (Lindsey 1978; Braun and Reif 1985; Figure 1B). The mean tailbeat frequencies in a typical thunniform swimmer, the kawakawa, *Euthynnus affinis*, are 4.57 and 7.03 Hz at swimming speeds of 40 cm s⁻¹ and 80–100 cm s⁻¹ respectively (Donley and Dickson 2000). Oscillations of the tail may induce recoil or lateral oscillations at the head, which 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* one way to reduce the anterior recoil forces (Blake 1983; Webb 1984; Reif and Weishampel 1986; Fish et al. 2003) is by increasing the surface area around the center of mass via the dorsal fin (Webb 1984), which increases the added mass and inertia at the anterior end of the animal (Fish et al. 2003). It is clear that the control structures in high-speed swimming vertebrates are of particular hydrodynamic importance. To this end the dermis in the dorsal fin was investigated for the first time in *C. carcharias* and indeed in sharks per se (Lingham-Soliar 2005a).

Transverse sections of the skin in the dorsal fin of the white shark, *C. carcharias* have shown two distinctive fiber organizations (Figure 5A). Unlike in the body of other sharks (Motta 1977) in which the fibers of the dermis all formed part of a crossed-fiber architecture, numerous layers of fibers in the dorsal fin of *C. carcharias* were steeply oriented in the same direction (in excess of 60°) and strained (prestressed) (Figure 5B). Furthermore in transverse section, the fibers are not organized in neat horizontal rows of fiber bundles of equal height but are tightly grouped together in staggered formation (bundles of varying height; Figure 5A). These fibers serve to facilitate rapid transfer of tension from fibers wound around the shark's body to the dorsal fin. With increases in speed, hydrostatic pressure within the shark increases (Wainwright et al. 1978) and fibers become taught around the body. The fiber tensions are directly transferred to the dorsal fin, making it stiff. Hence the increase in stiffness of the dorsal fin is achieved during fast swimming at the precise moment in time when the problems of yaw and roll are greatest. However, at the base of the dorsal fin the dermal fiber architecture was found to occur in layers of alternating oppositely fibers at low

fiber angles (Figure 5C). Functionally this enabled smooth bending of the dorsal fin during slow swimming. The fiber organization of *C. carcharias* while sharing some characteristics with other sharks, e.g., the tiger, *Galeocerdo cuvier*, and ragged tooth, *Carcharias taurus*, was found to be significantly more highly organized and more precisely associated with specialist functions of a dynamic stabilizer in the thunniform shark (Lingham-Soliar 2005a).

A study of the dermal fiber structure of the dorsal fin of *Stenopterygius* SMF 457 (Lingham-Soliar and Plodowski 2007) has shown striking similarities when compared with that of the dorsal fin of *C. carcharias* (Lingham-Soliar 2005a, 2005b). Two major types of fiber orientations were found. In the first, alternating layers of oppositely oriented fibers at the lower posterior part of the fin and lower middle are oriented at low to moderate fiber angles (35–45°) respectively (Figure 5D, F). This apparently allows greater freedom of fiber movements and facilitates reorientation toward a stress axis (Naresh et al. 1997; Lingham-Soliar 2005a, 2005b). In the second type, numerous fiber layers occur with fiber orientation in a single direction and at steep angles to the long axis of the ichthyosaur (Figure 5E). This fiber architecture was found toward the anterior and tip of the dorsal fin of *Stenopterygius* where torsional stresses were considered to have been greatest, a condition again similar to that seen in *C. carcharias* (Lingham-Soliar 2005a, 2005b). These fibers are predominantly in a single orientation, at 50–60° to the long axis, in numerous layers before a reversal in orientation, also maintained in several layers (Figure 5E). 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, 2005b).

The caudal fin

In non-lamnoid sharks the caudal fin lobes are distinctively unequal. The upper lobe is usually much larger than the lower and is, unlike the latter, supported by an extension of the vertebral column (McGowan 1992a, 1992b). In *C. carcharias* the dorsal and ventral lobes are subequal with the dorsal lobe only slightly larger than the lower and,

Fig. 4 Continued

of the finer fibers impressed over the thicker (see insets 1, 2, and 3 in (A) and in (B)). (C) Specimen PMU R435 showing fibers (class 1) on the body just below and anterior to the dorsal fin (well organized, cf. (A) and (B) and showing high fiber angles). (A), (B), and (C) modified from Lingham-Soliar 2001). (D) *Ichthyosaurus* GLAHM V1180a from the Lias of England. Although considerably decomposed, a cross-fiber (class 3) architecture (white arrows show 2 directions) is seen in two layers of the dermis preserved over the jaws of the ichthyosaur (after Lingham-Soliar 1999, courtesy of the Royal Society, London).

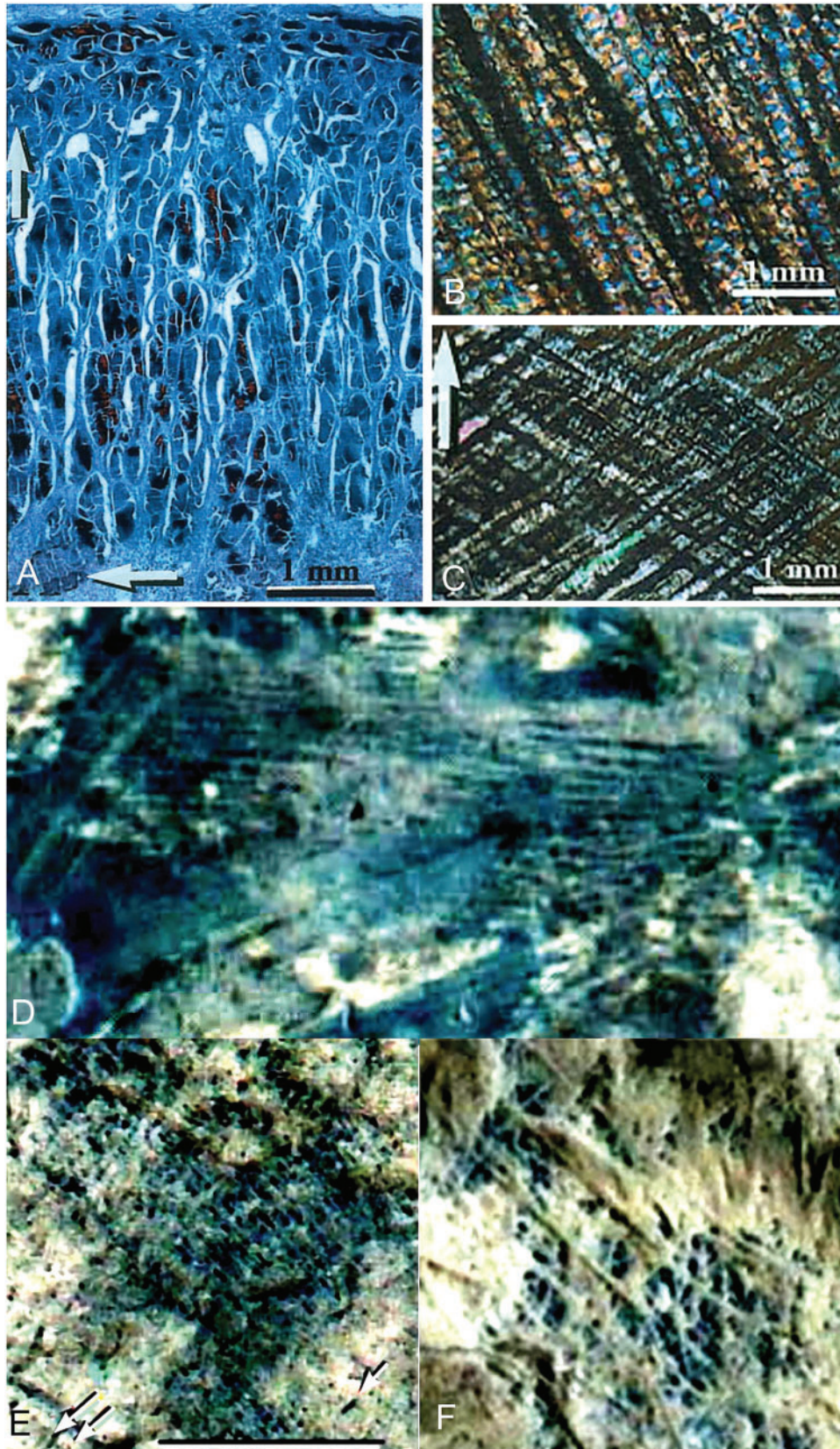


Fig. 5 *Carcharodon carcharias* (A–C) and *Stenopterygius* (D–F). (A) Thick stratum compactum with densely packed fiber bundles in staggered formation. (B) The fibers form thick bundles and are oriented at 60° to the long axis of the shark toward the central fin area. (C) Section just below the dorsal fin of *C. carcharias* showing lower fiber angles. (D) Fibers toward the base of the fin of *Stenopterygius* SMF 457 with low fiber angles, $\sim 35\text{--}40^\circ$. (E) Fibers occur in steeply angled right-hand orientations in several layers toward the central fin area. (F) Fibers of this ichthyosaur occur in right- and left-hand orientations ($\sim 50^\circ$) in some layers toward the central fin area.

as in other sharks, supported by an extension of the vertebral column.

It has been shown that dermal fibers of the stratum compactum of the dorsal lobe of the caudal fin occur in numerous distinct layers. In *C. taurus* and *G. cuvier* at one-third span the stratum compactum fiber layers are all of the same height in cross-section (Lingham-Soliar 2005b, their Figure 8) and separated by a thin sheet of cartilaginous tissue as also shown separating the fiber layers in the body of many non-lamnoid sharks (Motta 1977). The layers are more complex in *C. carcharias* and *I. oxyrinchus* (Figure 6A, B) than in other sharks and reflect a hierarchical development. Transverse sections of the dermis show that the fiber layers are organized into distinctive layers of fiber bundles that get progressively thicker deeper into the dermis. Each of these layers is separated by a layer of smaller uniformly sized fiber bundles rather than cartilaginous tissue (Figure 6A, B and inset). This strict demarcation of the major fiber layers is considered to enable free and independent fiber movements within each layer and to enable changes of fiber angles during these movements. Sagittal sections (parallel to the surface) of the stratum compactum have shown that fiber bundles in the dorsal lobe are oriented at 55–60° with respect to the long axis of the shark and in alternating left- and right-handed directions (Figure 6C). In the dorsal lobe, ceratotrichia are present only along the leading edge (embedded within connective tissue), apparently as reinforcement.

Stratum compactum 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. In sagittal sections the fiber bundles are oriented at angles of ~60°, generally in a single direction, i.e., lacking the left- and right handed helical pattern and rather resembling the architecture of the dorsal fin in *C. carcharias* (Figure 5A, B). The functional interpretation, as noted in the dorsal fin, is emphasis on stiffness rather than mobility. So effective is this second stiffening strategy that despite a lack of vertebral support in the ventral caudal fin lobe in lamnoid sharks, tensile tests on both lobes (Lingham-Soliar 2005b) have shown that stiffness is higher in the ventral lobe than in the vertebral-supported dorsal lobe, a condition predominantly achieved by dermal and subdermal collagen fibers. It was further proposed that any discrepancies in stiffness in the upper lobe compared with the ventral lobe may be redressed during high-speed swimming and increased hydrostatic pressure in the dorsal lobe (the ventral lobe is not subject to hydrostatic pressure) (Lingham-Soliar

2005b). This finding overturns a view prevalent in the literature for over half a century that the dorsal lobe of the caudal fin in sharks is stiffer than the ventral (Grove and Newell 1936; Ferry and Lauder 1996), probably assumed because of the sole presence of vertebral support in the former, further re-emphasizing the biomechanical function of the dermal cross-fiber architecture in animals.

The dorsal lobe of the caudal fin in *Stenopterygius* is the counterpart of the ventral lobe of the white shark. It is unsupported by the vertebral column but a remarkable 3-D preservation shows that it is packed with about eight layers of fibers with right-handed orientation before a reversed left-handed orientation also in numerous layers occurs (both orientations are about 45° and 55° to the ichthyosaur longitudinal axis) (Figure 6D, E). As we saw in the dorsal fin a mechanical explanation for the fiber architecture is a response to torsional and bending stresses. Fibers in the ventral lobe are poorly preserved but it is just discernable from some fibers at the base of the lobe that the fibers orient at low angles while toward the upper part of the lobe the angles increase to about 45°.

Findings of a highly organized cross-fiber architecture (with distinctive characteristics seen in lamnoid sharks as shown) and its association with stiffness in both the body and the dorsal and caudal fins of *Ichthyosaurus* and *Stenopterygius* are important because it has made possible a more comprehensive understanding of how this crucial design strategy contributes to the swimming efficiency of these thunniform vertebrates.

Caudal peduncle

The caudal peduncle in thunniform swimmers is a specialized structure designed to enable a constant angle of attack of the caudal fin during oscillations. This is achieved by a double-jointed or flattened (opposite to direction of caudal fin motions) caudal peduncle (Figure 7C), which tapers into a narrow “neck” as it connects with the caudal fin. This feature enables the anteriorly placed locomotory musculature to exert forces on the caudal fin with minimal bending of the body but rather by pulling on tendons that pass through the narrow peduncular “neck” just anterior to the caudal fin (Fierstine and Walters 1968; Lingham-Soliar 2005b; Shadwick 2005). Such a structure helps confine locomotory movements to the caudal fin. The caudal peduncle is a structure that also helps reduce anterior recoil forces by reducing the mass effect posteriorly during caudal fin oscillation (Blake 1983; Webb 1984; Reif and Weishampel 1986; Fish et al. 2003).

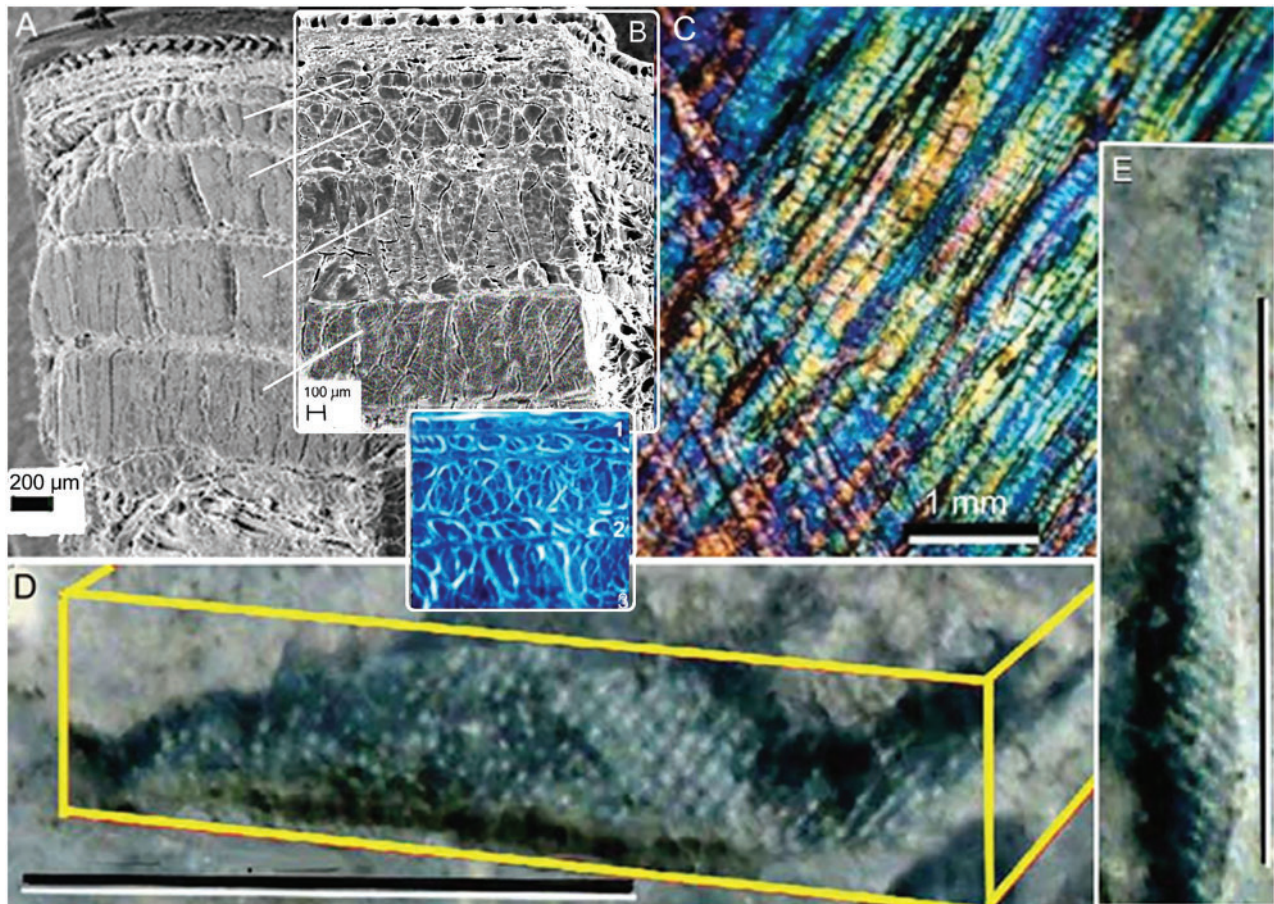


Fig. 6 SEM. Dermal fibers in the caudal fin of *Carcharodon carcharias* (A) and *Isurus oxyrinchus* (B). (A) (B) Transverse section at one-third dorsal lobe span of. Eight layers of fiber bundles, four thick layers alternating with 4 thin layers. Inset, histological transverse section in another specimen of *C. carcharias* showing a similar organization as in (A) and (B). (C) Sagittal section in *C. carcharias*. Collagen fibers in the stratum compactum of the upper lobe of the caudal fin of a specimen at about mid-span showing alternating left- and right-handed fibers at $\sim 60^\circ$ to the lobe base or body axis (after Lingham-Soliar 2005b). (D, E) Dermal fibers in the caudal fin dorsal lobe (lacking vertebral support) of *Stenopterygius* SMF 457, exposed in transverse section (almost 90° to the surface). (D) About eight layers of fibers oriented at about 45° (right-handed) to the ichthyosaur's long axis, preserved as a unique 3-D image. (E) Three to four layers of fibers oriented at $50\text{--}55^\circ$ (left-handed) (after Lingham-Soliar and Plodowski 2007).

In *C. carcharias* it was shown that stiffness is achieved principally by a thick layer of adipose tissue in the caudal peduncle ranging from 28% to 37% of its cross-sectional area and is reinforced by the dermal cross-fibered layers (Lingham-Soliar 2005b). Pabst (1996) suggested that very high fiber angles in collagenous fibers in the caudal peduncle of dolphins (secondarily aquatic mammals) serve to reinforce the peduncle and to act like a flexor retinaculum to keep the lateral tendons from bowstringing. Pabst (1996, 49) predicted that the skin in the caudal peduncle of lamnid sharks would also have a retinacular function, and that the skin fiber angles would be higher than those reported for slower swimming sharks ($45\text{--}50^\circ$) lacking a caudal peduncle. Sagittal

sections of the dermis overlying the caudal peduncle of *C. carcharias* has shown that fibers occur in oppositely oriented helical patterns with fiber angles greater than 65° , including in the thin parts of the skin in the lateral surfaces of the peduncle where it is highly compressed dorso-ventrally (Figure 3C). Below the dermis, sagittal and transverse sections show a dense fabric of collagen fibers around the adipose cells (Lingham-Soliar 2005b), very similar to the structural architecture of dolphin blubber (Hamilton et al. 2004).

In the lateral beating cycle of ichthyosaurs, the caudal peduncle if present would have been depressed dorso-ventrally as it is in *C. carcharias* (Figure 7C) and in the mako shark, *I. oxyrinchus*.

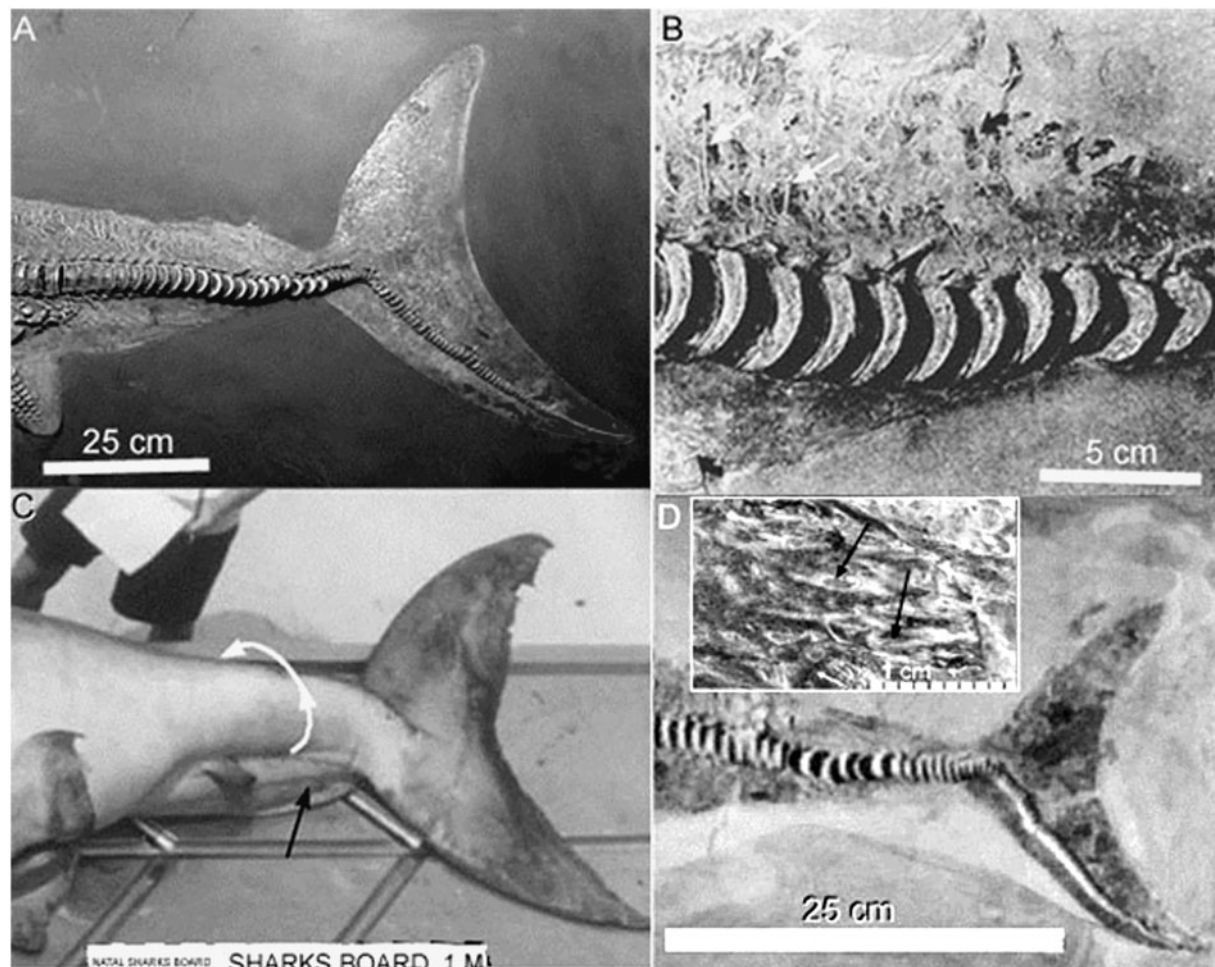


Fig. 7 *Stenopterygius quadricissus* (A, B, D). (A) Dorsolateral view of meshwork of filamentous fibers over surfaces of the body. Because of slight dorso-lateral compression the fleshy outline of the caudal peduncle is visible. (B) Thick fibers in the caudal peduncular area immediately anterior to the caudal fin. Note, the predominantly vertical orientations of the fibers despite preservational disturbance. (C) Caudal peduncle of *Carcharodon carcharias* twisted (left edge upward and right edge downward). (D) Specimen Re 1297/1 of *Stenopterygius* (view flipped horizontally to coincide with the other images). Inset shows preserved ligaments (modified from Lingham-Soliar and Reif 1998).

The problem with respect to identifying such a structure lay in the fact that virtually all Jurassic ichthyosaurs were preserved laterally compressed. This would mean that compression would theoretically occur on the thin edges (or “wings”) of the dorso-ventrally flattened caudal peduncle, rendering observation unlikely. However, *Stenopterygius* R 457 while predominantly laterally compressed has also shown some degree of dorso-ventral compression (Figure 1B, 7A). This has apparently resulted in a downward twisting of the “peduncular” region as evidenced by vertebrae in this region. We also see an apparent “swelling” of the soft tissue above this region. A reasonable interpretation is that the right “wing of the caudal peduncle was crushed during twisting and dorso-ventral compression while the left “wing” was twisted and displaced upward before being geologically compacted (Figure 7A). We can see exactly how

this could have happened in a large specimen of *C. carcharias* (Figure 7C), which was photographed as it lay on its right side. Although circumstantial it also seems no coincidence that in a number of ichthyosaur specimens, e.g., SMF 457 (Figure 7A) and GPIT RE 1297 (Figure 7D), the vertebrae in the “peduncular” region are displaced downward (Hauff and Hauff 1981) whereas some have been set straight by the preparator (Rupert Wild, former curator of Staatliches Museum für Naturkunde, Stuttgart; personal communication in 1994).

It is noteworthy that in the dermis of the “peduncular” region of SMF 457, fibers occur with high fiber angles (Figure 7B) as was predicted for thunniform swimmers (above). Finally, narrow-necking would have necessitated tendons to transfer the muscular forces to the caudal fin. A study (Lingham-Soliar and Reif 1998) has shown a concentration of

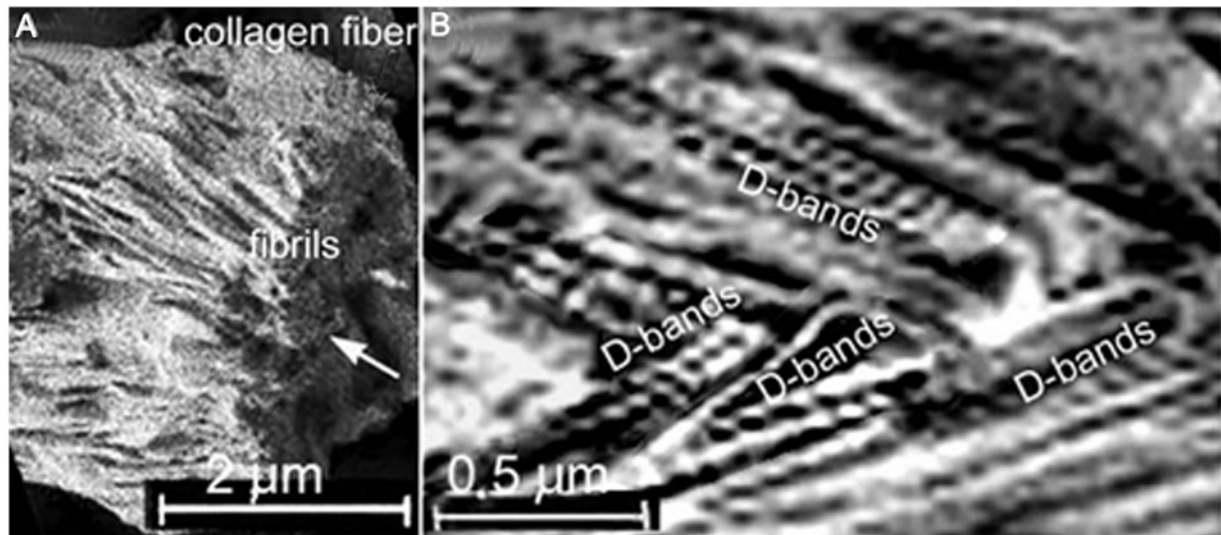


Fig. 8 Collagen fibers. (A) The sheared tip of a dermal fiber from *Ichthyosaurus* specimen GLAHM V1180a. The fiber is eroded but shows an angled cross-sectional view. Fibrils can be seen all the way to the fiber center. (B) Well-preserved D-bands or 67 nm repeat axial bands of the fibrils of GLAHM V1180a (Lingham-Soliar and Wesley-Smith 2008, courtesy of the Royal Society of London).

phosphatized tendons in the peduncular region of *Stenopterygius* (Figure 7D, inset).

Correlation of the paracrystalline array of tropocollagen monomers in the cross-fiber architecture of sharks and ichthyosaurs

The periodical *D*-band pattern is generally considered a unique ultrastructural feature shared by all fibril-forming collagens, which correlates with the intrafibril, paracrystalline array of tropocollagen monomers. The *D*-band has been identified graphically in shark skin collagen fibrils (Lingham-Soliar and Glab 2010). Although the near identical cross-fiber architectures in the white shark, *C. carcharias*, and the ichthyosaurs, *Ichthyosaurus* and *Stenopterygius*, suggest that they are comprised of the scleroprotein collagen (the main component of dermal tissue in vertebrates), it was in my view necessary to confirm this by investigation of the *D*-band periodicity.

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 nanophysical 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. This is the standard method for establishing type I collagen in both nascent and fossil material (Smith 1968; Kadler et al. 1996; Reichlin et al. 2005).

The SEM studies of fossilized soft tissue from *Ichthyosaurus* GLAHM V1180a have shown numerous component fibers and fibrils (Figure 8A). A dedicated search for *D*-bands ($n = 329$) in a number of fibrils ($n = 38$) revealed fibrils with the distinctive axial band periodicity of 66.12 nm (ave. $n = 38$, s.d. = 4.35) (Figure 8B) (Lingham-Soliar and Wesley-Smith 2008) consistent with the repeat *D*-band ultrastructure of type 1 collagen (Smith 1968; Kadler et al. 1996; Reichlin et al. 2005). The findings have shown conclusively that the fibers preserved in the ichthyosaur integument were undoubtedly collagenous and thus conclusively established another biological characteristic of ichthyosaurs consistent with that of other members of thunniform swimmers.

The evolution of the thunniform anatomy in lamnid sharks and Jurassic ichthyosaurs support the view that physical and hydromechanical demands provided important selection pressures to optimize body design for locomotion during vertebrate evolution (Donley et al. 2004). The review above demonstrates that lamnid sharks and Jurassic ichthyosaurs have converged to a much greater extent in morphological and functional adaptations than previously known and that their shared characteristics are more than skin deep.

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