

Taphonomic evidence for high-speed adapted fins in thunniform ichthyosaurs

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Abstract Ichthyosaurs have been compared with the fast-swimming thunniform groups of marine vertebrates, tuna, lamnid sharks, and dolphins, based on similarity of shape of the body and locomotory organs. In addition to shape, high-tensile stiffness of the control surfaces has been shown to be essential in maximizing hydrodynamic efficiency in extant thunniform swimmers. To date, there has been no evidence of a stiffening support system for the dorsal fin and dorsal lobe of the caudal fin in ichthyosaurs, the sole stiffening structure of the ventral lobe being an extension of the vertebral column along its leading edge. *Stenopterygius* SMF 457 is arguably the best soft-tissue preserved ichthyosaur specimen known. Here, we examine soft-tissue preservation in this specimen in the control surfaces and provide the first evidence of a complex architecture of stiff fibers in the dorsal and caudal fins. We find by comparisons and by analogy that these fibers provided a remarkable mechanism for high tensile stiffness and efficiency of the locomotory organs virtually identical to that of the great white shark, *Carcharodon carcharias*. It is the first mechanostudy of the control surfaces of a Jurassic ichthyosaur that adds essential evidence in support of the view that these forms were high-speed thunniform swimmers.

Keywords Ichthyosaur soft-tissue preservations · Fiber architecture · Caudal and dorsal fins · Tensile stiffness · Swimming efficiency

Introduction

The classic occurrence of similar highly derived shapes of the body and locomotory appendages in four groups of marine vertebrates classified with a thunniform swimming mode, i.e., Jurassic ichthyosaurs, tuna, lamnid sharks and dolphins (Lingham-Soliar 2005b), has fascinated biologists and engineers alike (Lighthill 1975). Yet, besides the similarity of shape of the dorsal and caudal fins in thunniform swimmers, we know very little of their deeper structure and, consequently, their efficiency in ichthyosaurs.

A large, highly stiffened dorsal fin in extant thunniform swimmers contributes an important mechanism for reducing the forces of yaw (rotation about the vertical axis) and roll (rotation about the longitudinal axis; Lingham-Soliar 2005a), while a highly stiffened, high-aspect ratio (AR) caudal fin contributes to an efficient oscillatory propeller (Lingham-Soliar 2005a–c).

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. In tuna, the dorsal and caudal fins are supported by bony spines (Drucker and Lauder 2001); in dolphins, these organs are de novo dermal structures, formed and supported only by connective tissue (Pabst 2000), and in sharks, cartilaginous radials provide skeletal support solely at the base of the dorsal fin, while the ventral lobe of the caudal fin entirely lacks skeletal support (Lingham-Soliar 2005a,c). However, hundreds of

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Fig. 1 *Stenopterygius quadricissus* SMF 457 (Senckenberg Museum), approximately 2.3 m long, showing a large dorsal fin and high-aspect-ratio caudal fin, reminiscent of the thunniform white shark, *Carcharodon carcharias*



ichthyosaur specimens have failed to show any trace of skeletal support for the dorsal fin or the dorsal lobe of the caudal fin.

A new model involving precise collagen architectural constructions was proposed for reinforcement of the control surfaces of sharks based on anatomical and load test analysis, showing that the skin in the dorsal and caudal fins of the white shark, *Carcharodon carcharias*, contributes about 50% of the tensile stiffness (Lingham-Soliar 2005a,c), and on a study in which the engineering principle of thin-cylinder fiber, reinforcement was extended to other shapes in nature (Lingham-Soliar 2005c; Clark and Cowey 1958). As in sharks, a collagenous fiber architecture occurs in the integument of *Stenopterygius*, over the head and body (Lingham-Soliar 1999, 2001). The dorsal and caudal fins were not previously studied.

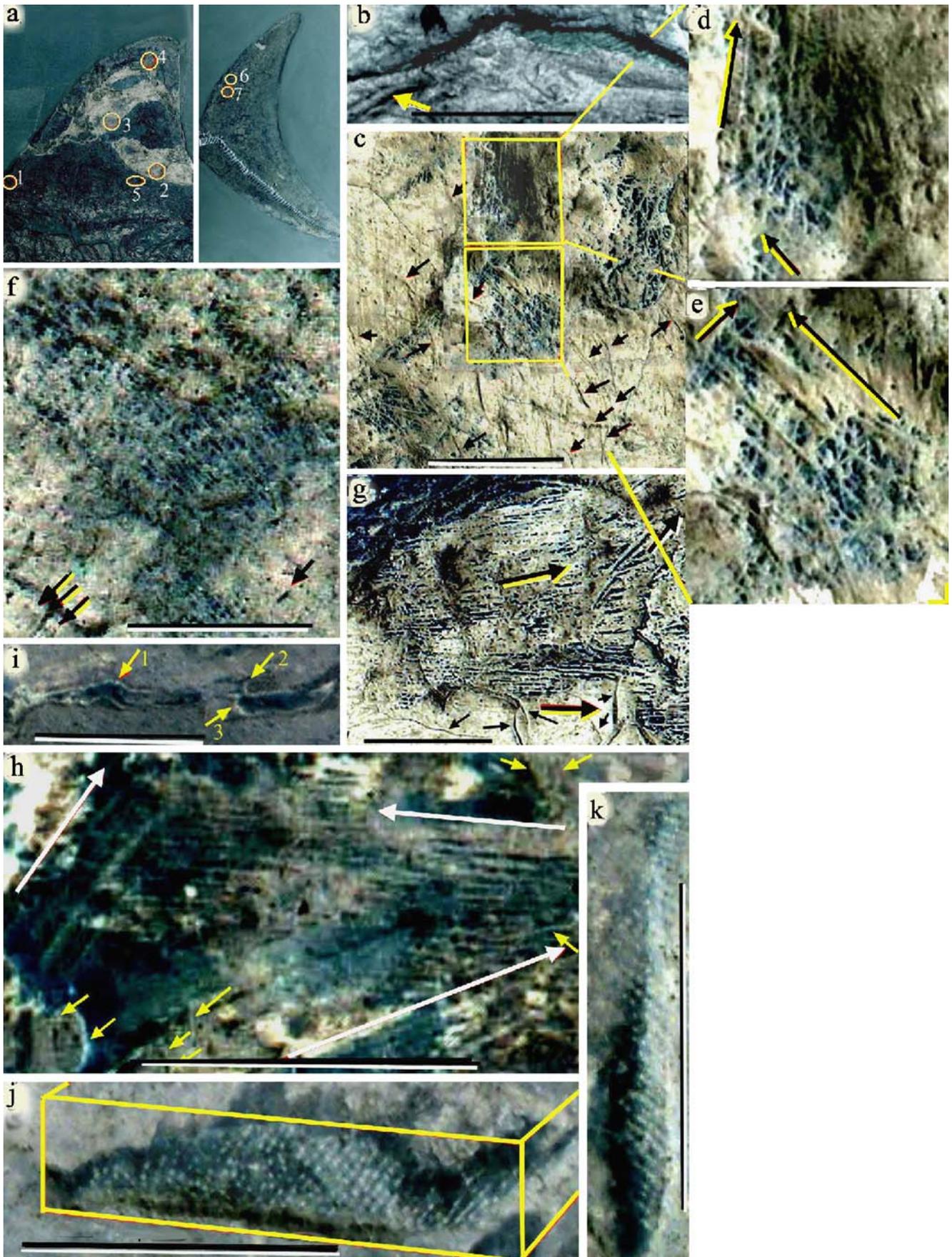
Our study of the fiber architecture in the dorsal and caudal fins of the Posidonia Shale ichthyosaur *Stenopterygius* SMF 457 (Fig. 1) depends on extraordinary soft-tissue preservation. As Martill (1995, p. 897) states, such ichthyosaur preservations “offer a unique opportunity to examine aspects of ichthyosaur morphology, biomechanics, physiology and ecology...,” adding “the most spectacular specimens are from the Posidonia Shale.” Here, we are able to make close structural and functional comparisons with the counterpart organs of *C. carcharias* (Lingham-Soliar 2005a,c) that are seldom possible in a fossil animal.

Materials and methods

The biology (excluding that of the control surfaces), geology, and taphonomy of *Stenopterygius* SMF 457 (Senckenberg Museum, Germany) from the *Posidonia* Shale of Holzmaden was described in detail previously (Lingham-Soliar 2001; 2003). Included there are descriptions and comparisons with two other ichthyosaur specimens, *Stenopterygius* PMU R435 (Paleontological Museum, Uppsala; Holzmaden) and *?Ichthyosaurus* GLAM V1180a (Hunterian Museum, Glasgow; Lower Lias, Gloucestershire, UK; for detailed description, see Lingham-Soliar 1999). The “exceptional

preservation of ichthyosaurs of the Posidonia Shale” is attributed to rapid mineralization of soft tissue in a soupy substrate medium (Martill 1993, p. 77). Martill (1995, pp. 898–900) states that soft tissue in the Sinemurian ichthyosaur is represented by “buff coloured, slightly fibrous material...probably phosphatic” and “closely resembles phosphatic material found in Holzmaden ichthyosaurs.” Similar phosphatization of fibers was found in *?Ichthyosaurus* GLAM V1180a despite highly different preservational conditions, the latter preserved in a mudstone nodule (Lingham-Soliar 1999). All fibrous structures are in relief, giving a near three-dimensional appearance. The only comment we are aware of on the rare possibility of prokaryote replacement of soft tissue in an ichthyosaur, in which detail is lacking, was even there later considered

Fig. 2 *S. quadricissus* SMF 457. **a** Dorsal fin (left) and caudal fin (right); red circles mark sites described. **b** Cut in fin shows underlying fibers. **c** Four areas of well-preserved helical fibers in several layers in site 2 (see detail in **d**). Arrows show fibers in the decomposing outermost layer, many of which have started to lose their tension and become more sinuous. **d, e** Fibers occur in steeply angled right- and left-hand helices in several layers (arrows show main fiber directions). **f** Left-hand-oriented fibers in site 3. In the bottom left of the picture, traces of an overlying layer (degrading) with right-hand-oriented fibers can be seen (arrows). **g** Fibers in site 4. Large arrows show direction of fibers in three layers, two at low fiber angles, and one at high (in traces of the layer); small arrows show decomposing fibers in outer layer. **h** High-tensile fibers near the fin base in three to four layers, two show low fiber angles and one, high (long arrows); short arrows show fibers in decomposing outermost layer. **i** Fibers within the outermost layer starting to degrade and become sinuous (arrow 1) with occasional overlying fibers (arrows 2 and 3); note how they become uncovered along the fiber length and not across, a process referred to as ‘tramlining’ (Lingham-Soliar in Feduccia et al. 2005). **j** Fibers (site 6) 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. **k** In the caudal fin, dorsal lobe (site 7), about 1 cm away from site 6, three to four layers of fibers oriented at 50–55° (left-handed) occur. Note that colors are reversed by polarizing filter to show fine detail. Scale: **b, f, i, h, j, k**=1 cm; **c, g**=2 cm



unlikely by the same author (Martill 1995, p. 902 and references therein) and needs no further comment.

Underlying this study is the fact that almost all the fibers examined are straight, a reasonable indication of a remarkable degree of fiber tension and fin stiffness right up to the point of death and fossilization (Lingham-Soliar in Feduccia et al. 2005). It is also a reliable indication that these fibers are preserved in situ. Loss of tensile stiffness is usually reflected by curvature of the fibers, e.g., seen in decomposing dolphin and dinosaur skin (Lingham-Soliar in Feduccia et al. 2005) and here in the decomposing outermost layers of the dorsal fin (e.g., Fig. 2c,i,h; arrows). Thickness of fibers ranged from 180 to 220 μm ($n=50$). Note, the term fiber actually refers to fiber bundle (Lingham-Soliar 2005a,c).

The five areas of fibers investigated in the dorsal fin are considered a good representation of the entire fin (Fig. 2a). The dorsal lobe of the caudal fin also showed a number of areas with comparable fibers, but because of more severe degradation (a term used here to include biological and mechanical erosion), descriptions are, to a greater extent, made with respect to preservations in the dorsal fin. Most sections are tangential (Lingham-Soliar 2005a), i.e., lie parallel to the skin/organ surface, the common observations in fossils. 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 an astonishing level of integumental information that is seldom possible in a fossil.

Site 1 (Fig. 2b) lies close to the anterior base of the fin and consists of a narrow longitudinal excavation, probably a pre-fossilization cut in the fin within which can be seen diagonally oriented fibers (Fig. 2b). The fibers appear several millimeters below the fin's surface and show minimal degradation and distortion.

In Fig. 2c, site 2, four patches of soft tissue occur, which includes a fine preservation of fibers (Fig. 2d,e) that is reminiscent of fresh tissue rather than of a 200-my fossil. Fibers from several layers orient in left- and right-handed directions at angles ranging from 45° to 70° . The surrounding overlying area (white, in reality black) is where active decomposition was occurring at the time of fossilization in which traces of decomposing, sinuous fibers are apparent (Fig. 2c, arrows).

The third site (Fig. 2f) is located in the central area of the fin. The surface has almost entirely degraded, exposing a deeper layer of fibers. The fibers are predominantly left-hand oriented at 50 – 60° to the long axis. In the degraded upper layer near the corners of the section, traces of right-handed fibers are discernible (Fig. 2f, arrows).

Figure 2g shows fibers in site 4, preserved near the tip of the dorsal fin (Fig. 2a). The fibers are mainly right-hand oriented in two layers, oriented at acute angles to the long axis, i.e., almost parallel. In addition, traces of fibers oriented at steeper angles (about 70°) are present. The outermost (white) degraded layer shows traces of sinuous fibers that have lost their tension.

Fibers in site 5 occur near the base of the dorsal fin (Fig. 2h) in at least three distinct layers; in two, the fibers are acutely angled (about 25° to the long axis) in opposite left- and right-hand orientations, and in one, steeply angled. Figure 2i shows fibers typical of the more severely degraded outermost layer in which fiber tension is lost (arrow 1). The manner in which underlying fibers become exposed, with the erosion propagating or 'tramlining' (Lingham-Soliar in Feduccia et al. 2005) along the fiber rather than across, is apparent (Fig. 2i).

Fibers in site 6 in the dorsal lobe of the caudal fin (lacking vertebral support) occur in transverse section almost 90° to the fin surface while the section is partially

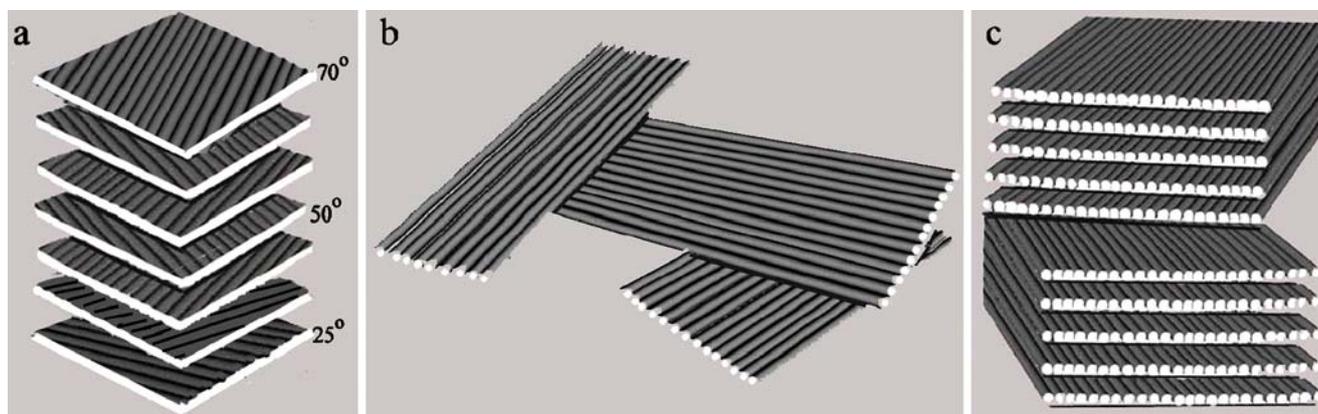


Fig. 3 Schematic views of major fiber constructions in the control surfaces of *Stenopterygius*. **a** Exploded view of fibers in alternate layers of left- and right-handed orientations. Fiber angles differ from steep to shallow angles in the layers (range shown 25 – 70°). **b** At the

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. **c** Numerous layers with fibers oriented in the same direction before a reversal in direction

sheared at a more acute angle to the surface. This provides a remarkable 3-D view of approximately eight layers of fibers (Figs. 2j, 3c), right-hand oriented at about 45° to the ichthyosaur's long axis. About 1 cm away at site 7, a narrower section cut at an angled transverse plane shows fibers in about three to four layers deep in opposite left-hand orientation at about 55° to the ichthyosaur's long axis (Figs. 2k, 3c).

Discussion

The importance in thunniform swimmers of a large, deep, highly stiffened dorsal fin for stability and a high-AR, highly stiffened lunate tail for fast, efficient propulsion was investigated and reviewed recently (Lingham-Soliar 2005a,c). However, it was only recently shown how the vital component of stiffness of the control surfaces in thunniform sharks is achieved—predominantly by dense bundles of straight collagen fibers (Lingham-Soliar 2005a,c). As a consequence of extraordinary preservation of soft tissue showing fibrous structures in *Stenopterygius* SMF 457, we are able to show by analogy a similar stiffening role of fibers in the control surfaces of ichthyosaurs to that of thunniform sharks and add to our knowledge on ichthyosaur hydrodynamics. It is significant that collagen fibers when straight, as in the case of these fins (as in those of sharks), have an exceedingly small stretch when placed under tension and would contribute to a rigid structure.

Two principal mechanical strategies counteract the bending stresses in the dorsal and caudal fins in both vertical and horizontal planes. First, a system of fibers with diagonal or bias arrangement (Fig. 2c–f) of alternating left- and right-hand-oriented fibers provides stiffness in shear that functions to reinforce the fin as in fiber-reinforced thin cylinders (Lingham-Soliar 2005c; Clark and Cowey 1958; Wainwright et al. 1976). The details (Fig. 2d,e) show a rare view into the integument several fiber layers deep in which neighbouring layers differ in the helical angles (ranging about 45–70°) and directions (left- and right-handed), reminiscent of the helicoidal model of chitin fiber reinforcement in arthropod cuticle (Neville and Luke 1969; Fig. 3a). The helical orientations have also been shown in shark dermis to allow greater freedom of fiber movements that facilitate reorientation toward a stress axis (Lingham-Soliar 2005a,c; Naresh et al. 1997). Stiffness in the lateral plane is achieved by fibers that parallel or orient at acute angles to the long axis of the ichthyosaur (Fig. 3b). This reinforcement was found at the base and tip of the dorsal fin where torsional stresses were probably greatest (Figs. 2g,h, 3b). Second, in the 3-D images from the unsupported dorsal lobe of the caudal fin (Fig. 2j), fibers follow the same orientation in about eight layers (right-

handed) before a reversal (Fig. 2k) in orientation (left-handed), a structural architecture (Fig. 3c) considered to have functional implications connected with control surfaces dedicated to stiffness and stability during locomotion (Lingham-Soliar 2005a,c). The first strategy was found in the integument of sharks, overlying the body (Motta 1977; Wainwright et al. 1978) and dorsal and caudal fins (Lingham-Soliar 2005a,c), but the second strategy was found solely in the dorsal fin and the unsupported ventral lobe of the caudal fin in sharks (Lingham-Soliar 2005a,c). So effective is this second stiffening strategy that despite a lack of vertebral support in the ventral caudal fin lobe in sharks, tensile stiffness (entirely achieved by dermal and subdermal collagen fibers) is significantly higher than in the vertebral-supported dorsal lobe (Lingham-Soliar 2005c), overturning 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). This is hardly surprising given that collagen fibers constituting just 6% thickness of the dorsal lobe of sharks produces about 50% of its mechanical stiffness (Wainwright et al. 1978, Lingham-Soliar 2005c) and given that the ventral lobe comprises virtually 100% collagen fibers (Lingham-Soliar 2005c). Finding a fiber architecture representing the second strategy of fin stiffness in the unsupported (with respect to vertebral support) dorsal lobe of the caudal fin of *Stenopterygius* is considered highly significant.

Collagen is the basic structural fiber of the animal kingdom. Although a great deal of research has been carried out on the biology and chemistry of collagen, resulting in an immense literature, we are only beginning to understand the complex architectural arrangements of the fibers in dermal and subdermal tissue and their functional significance (Lingham-Soliar 2005a,c; Pabst 2000; Feduccia et al. 2005; Motta 1977; Wainwright et al. 1978). The control surfaces of *Stenopterygius* are examples of how basic fibers of collagen are organized in complex architectural structures (Fig. 3a–c) that enable a range of engineering strategies to deal with different stresses at different points of the structure. Rare anatomical evidence presented here on the control surfaces provides fundamental support for the concept of ichthyosaurs as fast-swimming marine vertebrates.

A study of the structural complexities involving collagen fibers in living and fossilized animals will help us to understand their functional significance and wider adaptive roles in nature. Fossilized soft tissue is difficult to interpret, and it is only through increased knowledge of living and extinct systems and of the decay processes, as demonstrated here, that we may achieve a better understanding (Briggs 2003). Using such rigorous principles of research may prove invaluable in understanding soft-tissue preservation associated with some of the famous Chinese dinosaurs.

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References

- Briggs DEG (2003) The role of decay and mineralization in the preservation of soft bodied fossils. *Annu Rev Earth Planet Sci* 31:275–301
- Clark RB, Cowey JB (1958) Factors controlling the change of shape of certain nemertean and turbellarian worms. *J Exp Biol* 35:731–748
- 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
- Feduccia A, Lingham-Soliar T, Hinchcliffe JR (2005) Do feathered dinosaurs exist? Testing the hypothesis on neontological and paleontological evidence. *J Morphol* 266(2):125–166
- 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
- Grove AJ, Newell GE (1936) A mechanical investigation into the effectual action of the caudal fin of some aquatic chordates. *Ann Mag Nat Hist* 17:280–290
- Lighthill J (1975) *Mathematical biofluid dynamics*. SIAM, Philadelphia
- Lingham-Soliar T (1999) Rare soft tissue preservation showing fibrous structures in an ichthyosaur 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? *Neues Jahrb Geol Paläontol 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 allometry in the white shark *Carcharodon carcharias*: implications for locomotory performance and ecology. *Naturwissenschaften* 92:231–236
- Lingham-Soliar T (2005c) Caudal fin in the white shark, *Carcharodon carcharias* (Lamnidae): a dynamic propeller for fast, efficient swimming. *J Morphol* 264:233–252
- Martill DM (1993) Soupy substrates: a medium for the exceptional preservation of ichthyosaurs of the Posidonia Shale (Lower Jurassic) of Germany. *Kaupia* 2:77–97
- Martill DM (1995) An ichthyosaur with preserved soft tissue from the Sinemurian of southern England. *Palaeontology* 38:897–903
- Motta PJ (1977) Anatomy and functional morphology of dermal collagen fibers in sharks. *Copeia* 1977:454–464
- Naresh MD, Arumugam V, Sanjeevi R (1997) Mechanical behaviour of shark skin. *J Biosci* 22:431–437
- Neville AC, Luke BM (1969) Model for chitin–protein complexes in insect cuticle. *Tissue Cell* 1:689–707
- Pabst DA (2000) To bend a dolphin: convergence of force transmission designs in cetaceans and scombrid fishes. *Am Zool* 40:146–155
- Wainwright SA, Biggs WD, Currey JD, Gosline JM (1976) *Mechanical design in organisms*. E Arnold, London
- Wainwright SA, Vosburgh F, Hebrank JH (1978) Shark skin: function in locomotion. *Science* 202:747–749