Rare soft tissue preservation showing fibrous structures in an ichthyosaur from the Lower Lias (Jurassic) of England

Theagarten Lingham-Soliar

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow 117868, Russia (lenin33@paleo.ru)

Rare soft tissue preservation of the skin of an ichthyosaur which includes fibrous structures is redescribed. The redescription and reinterpretation of the Lower Lias ichthyosaur specimen GLAHM V1180a given here shows two superimposed layers of fibres extending in opposite directions at angles of *ca.* 35° to the animal's long axis. This new data contributes to our understanding of the integument of ichthyosaurs, i.e. its strength and possible smoothness. Such information may be significant in interpretations of ichthyosaur locomotion.

Keywords: soft tissue; ichthyosaur skin; fibrous structure; hydrodynamics

1. INTRODUCTION

The skin forms the outermost covering of most vertebrates and is the first line of protection or shield from mechanical force and environmental stresses for the underlying tissues (Vincent *et al.* 1991). Thick collagenous tissues in the dermis possess mechanical properties suited to the function of protection. In addition, the collagenous fibres in a number of marine animals provide the potential for minimizing surface deformation. This is of particular significance in the reduction of frictional drag during swimming (Fish & Hui 1991; Fish 1993). Although there are a number of ichthyosaur specimens with fossilized soft tissues, notably from the Lower Jurassic Posidonia Shale of Southern Germany, so-called skin preservation is in fact often decayed and transformed soft tissue. This material may outline the body as a black film (Wild 1990; Martill 1993). While such specimens provide valuable information on the hydrodynamic body and tail shapes of ichthyosaurs, e.g. *Stenopterygius*, information on actual skin structures is rare (e.g. Martill 1995; Lingham-Soliar & Reif 1998). Thus, an earlier description (Delair 1966) of structures preserved in a layer of the skin of an ichthyosaur (*Stenopterygius*) is considered important.

Specimen GLAHM (University of Glasgow, Hunterian Museum) V1180a came from the Lower Lias of the Severn Valley in Gloucestershire. Since *Stenopterygius* is at present reported only from the Toarcian, the specimen (differing from *Stenopterygius* in, for example, tooth morphology) is probably the Lower Lias species *Ichthyosaurus* (see McGowan 1973). This is the first record of skin with fibres in a Lower Lias ichthyosaur.

Delair (1966) described the fibrous elements in GLAHM V1180a as consisting of 'thread-like strands' in an area of preserved skin on the surangular. Here I present a redescription with new interpretations which shed important light on the outer integument of ichthyosaurs and its possible significance in the efficiency of high velocity swimming.

2. MATERIAL

Specimen GLAHM V1180a lies within a mudstone nodule and consists of a partially preserved head which lacks the anterior extremities of the jaws and parts of the posterior lower jaw and posterior skull. The skull is *ca.* 40 cm long and the entire length of the animal is estimated at *ca.* 180 cm (head to body ratio of *ca.* 1:4.5). The head has been split vertically in the nodule in the region of the right sclerotic ring to produce two parts, specimens GLAHM V1180a and the less well-preserved GLAHM V1180b. Figure 1 shows the internal (medial) view of the right side of the skull of GLAHM V1180a. The external (lateral) right side of the skull lies against the matrix. The counterpart nodule, specimen GLAHM V1180b, essentially contains the left side of the skull. As it split from GLAHM V1180a it removed a fragment of the right surangular and dentary, thereby exposing the preserved soft tissue from its external surfaces against the rock matrix (GLAHM V1180a, figures 1 and 2). It is important to note that the fibres described here lie on the rock matrix. Although GLAHM V1180b is poorly preserved (not shown), traces of fibres are visible on the external (lateral) surfaces of parts of the surangular and dentary (corresponding to the areas of exposed fibres on the matrix). Thus, there is no doubt that the tissues are connected with the external (lateral) covering of these bones.

Unfortunately, because of the small quantity of the preserved soft tissue in GLAHM V1180a and the fact that sample preparation for scanning electron microscopy requires fragmentation of large specimens to produce stub-sized samples (Allison 1988a), it was not possible to analyse the chemical composition of the material from such a prized specimen. However, a reasonable guess can be made as to the nature of the transformation of the original biomolecules of the preserved tissue. The preservation of more volatile structures, e.g. muscle fibres, requires exceedingly rapid mineralization and, as a result, is frequently restricted to phosphatic transformation (Allison 1988b) or clay templating (Gabbott 1998). The buff-whitish colour of the preserved soft tissue in GLAHM V1180a is consistent with replacement by calcium phosphate. Such mineralization is

Figure 1. The partially preserved head of the ichthyosaur *?Ichthyosaurus* GLAHM V1180a ($\times 0.65$). There are strips of tissue that were previously interpreted as fibre strands on the rock matrix (surangular area).

known in ichthyosaur specimens from both the Lower Lias of England and the Posidonia Shale of Germany (Martill 1993; Lingham-Soliar & Reif 1998).

3. DESCRIPTION OF THE SOFT TISSUES

Delair's (1966) description referred to only one layer of fibres. The present study proposes that there are two (a layer of apparently thick strands which Delair (1966) described and a layer of thin fibres in his 'intervals' which he made no reference to). An outline of Delair's (1966) description is therefore given so as to distinguish clearly which of the two layers of fibres it is that is being referred to. Note that, in Delair's (1966) figure 3, his $\times 2$ is incorrect and should be $\times 6$ (cf. the natural size in his figure 2).

Delair (1966) described the fibrous elements of the skin overlying the surangular (preserved on the rock matrix) as consisting of 'separate fine thread-like strands of organic matter arranged in more or less parallel rows' (p. 576a) in a gently downward curving course (see fig. 2, Delair 1966); each strand is a continuous unit. Their density 'per centimetre varies between four and five strands' (Delair 1966, p. 576a). These parallel fibres occur in approximately parallel groups according to Delair (1966), and each group is separated by 'small intervals of irregular but predominantly elongate shape' (p. 576b, figs 2 and 3).

We need to be certain as to which of the two types of fibres it is that Delair (1966) referred to. This can be resolved fairly simply. Fig. 3 in Delair (1966) shows what are apparently his thick whitish 'fibres' and the thinner

fibres that lie below them. These thick whitish fibres are almost exactly $4\text{--}5\text{ fibres cm}^{-1}$ as Delair (1966, p. 576, fig. 3) stated; long arrow in figure 2a points to one of Delair's (1966) fibres. Thus, there can be no doubt that these are Delair's (1966) fibres. The areas below and between these thick fibres were dismissed by Delair (1966) as 'small intervals' without reference to the fine fibres (my second layer).

There are two important objectives of the present study: (i) to show that the fibres that Delair (1966) described are in fact not fibres at all but elongated strips of tissue, and (ii) to show from the surangular area and dentary that the preserved tissue of GLAHM V1180a consists of two superimposed layers of fibrous structures and not one as Delair (1966) inferred. These are layers 1 (incorporating Delair's (1966) fibres) and 2 (consisting of the fine fibres lying below layer 1, i.e. the outermost layer; figure 2a,b).

(a) *Layer 1*

This layer is in closest contact with the surangular and dentary bones and contains the fibres identified by Delair (1966). Close examination shows that what Delair (1966) described as 'separate, fine, thread-like strands' (p. 576a) are actually elongated strips of tissue. These strips vary in length and width. Under higher magnification (*ca.* $\times 5.5$) they are seen to be comprised of 'stubs' (i.e. degraded fibre remnants varying between 0.5 and 2.0 mm long) of compactly arranged fibres that extend diagonally to the length of the preserved strips of tissue (marked by arrows in figure 2a). In certain areas the fibres can be seen to extend even further than the narrow bands of tissue they

Figure 2. Detail (*ca.* $\times 5.5$) of most of the tissue preserved on the rock in the surangular area. (a) The fine fibres of layers 1 (in strips) and 2 (*ca.* $40 \text{ fibres cm}^{-1}$). The long strands can clearly be seen between the strips of layer 1. The long arrows show two strips of tissue that Delair (1966) mistook for fibres. A strip (mid-upper) has decomposed more and shows some of the fibres (indicated by small arrows) more clearly. In addition, the bottom right of the picture (demarcated) gives a hazy view of the cross-wise arrangement of the fibres of the two layers. The semicircle on the left shows the well-preserved fibres in layer 2. The circles show breaks in the fibres of layer 2 and the dark matrix below. (b) Tissue towards the left of the preserved area showing fibres curving more to the horizontal. The demarcated area on the left shows the well-preserved fibres of layer 2 while the semi-circle shows degraded fibres. Scale bar, 1 cm.

are normally confined to (e.g. the small arrows show a few in figure 2a). There are *ca.* $40\text{--}45 \text{ stubs cm}^{-1}$. Their thickness is measured as being *ca.* 0.1 mm (this can only be a rough estimate since it is not known how much erosion or, conversely, swelling the fibres have been subjected to). The roughly parallel strips of tissue extend at an angle of *ca.* 40° to the long axis of the lower jaw.

Although it is difficult to measure the angles of the short stubs of fibres in these narrow strips of tissue, in places where they extend a little further they are seen to extend *ca.* $25\text{--}30^\circ$ in a posterodorsal–anteroventral orientation.

The elongated strips of tissue overlie a second layer of fine thread-like fibres within Delair's (1966) small intervals, which are identified here as layer 2.

(b) Layer 2

This is the outermost of the two layers, and lies furthest from the bone and directly upon the rock matrix. It consists of compactly aligned fibres with a density of 40–45 strands cm^{-1} . The fibres' thickness (*ca.* 0.1 mm), density and colour are similar to those of the fibre stubs in the overlying layer 1. These fibres extend at angles of *ca.* 30–36° to the long axis of the lower jaw, but in the opposite direction to those of the overlying layer, i.e. in an anterodorsal–posteroventral orientation. At the upper margins of the preserved area of tissue, particularly on the most anterior part of the surangular (figure 2*b*) and dentary area, the fibres curve to follow the longitudinal axis of the lower jaw. This curvature of the fibres is less marked in the preserved skin near the posterior part of the surangular (figure 2*a*).

The curvature of the fibres, particularly in the area of the dentary where they follow a near horizontal direction, may be a taphonomic artefact produced by vertical squashing of the skin during the taphonomy of the animal and the skin (figure 2*a,b*). However, it is more likely that it is a primary feature of the integument and represents the natural orientation of the fibres over the dentary. Because of the ichthyosaur's gape the fibres would either have to have stopped at the edges of the dentary and anterior surangular or to have curved to follow the longitudinal axis of the jaw (figure 2*c*). The interception of fibres or strong curvature is known in Recent animals. In sharks, for instance (Motta 1977), the helical path of the fibres is interrupted where they intercept the fins. They also stop short of the edges of the caudal fin. Hebrank & Hebrank (1986) noted that, in tuna, in some cases the helical fibres of the fin may curve as they suddenly change pitch near the dorsal and ventral midlines. In the cetacean *Delphinus delphis* the thick vertical fibres of the dorsal fin (important in stiffening the fin since there is no skeletal support) curve strongly towards the horizontal along the posterior edge and tip of the fin (Burne 1952, p. 9 and fig. 3*A*).

Despite the poor preservation of layer 1, it seems unlikely that there was any interweaving of fibres between the two layers because of the close spacing of the fibres. In sharks interweaving of crossover fibrils (from one layer to another) occurs in some layers of fibres but not in others (Motta 1977).

It is easy to see why Delair (1966) interpreted the elongated patches of tissue as individual fibres because of their regular orientation in near parallel rows (Delair 1966, fig. 2). However, the very fine, dense fibres lying below are apparent even in his fig. 3 and are a significant omission.

4. DISCUSSION**(a) The effects of the taphonomic processes on fibre preservation in GLAHM V1180a**

Numerous critical conditions are required for the fossilization of soft tissues (e.g. Allison & Briggs 1991; Martill 1993) and the preservation of one type of organic material rather than another may sometimes even appear incongruous. In GLAHM V1180a, preservation of the fibres apparently occurred when parts of the skin were in contact with the (mud) matrix during the animal's taphonomy (note that strands of fibres were also

preserved on the rock matrix in *Stenopterygius* SMF (Senckenberg Museum, Frankfurt) 457; see below). Such preservation of the outermost layer of the skin compared to deeper layers may appear incongruous. The sediment is frequently a good source of bacteria and electron donors for decomposition. Aerobic respiration of organic carbon is commonly considered to be a more rapid means of biodegradation than anaerobic decay. Nevertheless, a number of conditions may slow down microbial decomposition in the sediment, e.g. a tough, waterproof skin, anoxia (equivocal, but it may promote soft part mineralization; Allison & Briggs 1991), protection from scavengers and high or low pH. In a classic study on the decomposition of thousands of large vertebrate carcasses, Weigelt (1989) showed that, in many animals drowned and partially buried during floods, the skin was preserved intact and that decomposition proceeded from within the animals. In actualistic experiments, Allison (1988*b*) showed that anaerobic decay of soft bodied and highly skeletized organisms can be extremely rapid. Apart from the gut, the mouth cavity and the teeth are a good source of bacteria and may facilitate bacterial decomposition from within the skull (see Halstead (1974) for bacterial decay of the teeth and skull in *Homo rhodesiensis*) with the skin furthest away probably the last to suffer. Interestingly, of the two layers in GLAHM V1180a, the innermost (layer 1) is degraded most.

The peculiar preservation of the nearly parallel strips of strand-like tissue in layer 1 in GLAHM V1180a is puzzling. A possible explanation is that the strips may have resulted from post-mortem creasing of the skin (see Buckland 1836; Martill 1987). Wrinkling of the skin produces 'peaks' and 'troughs' (figure 3*b*). The patches of preserved tissue (layer 1) in GLAHM V1180a represent the troughs, i.e. areas suffering the least 'degradation' or damage (figure 3*a,b*). The greatest degradation on the peaks would have exposed the underlying layer. How did this 'erosion' occur? Mechanical abrasion of the peaks by, for example, sediment either soon after death or after fossilization seems improbable since the creased layer (layer 1) lies innermost (in terms of the animal), i.e. within layer 2 (outermost) which shows no signs of creasing or folding. A possible explanation for the degradation is that the peaks of fossilized tissue were destroyed or removed (or both) during splitting of the nodule. Some of this tissue may represent the poorly preserved fibres in the counterpart nodule GLAHM V1180*b*. A more complex explanation is that the peaks of the creased internal layer of the animal (layer 1) were in closest contact with the decomposing tissue (assuming that decomposition proceeded from within the mouth cavity; see figure 3*b*). Hence, degradation would have started on the peaks just prior to being halted by mineralization. This left patches of tissue in the troughs of the wrinkled layer in near parallel rows (consistent with creasing in a layer that loses its tension).

However, an alternative proposal (anonymous referee) is that the elongated patches or strips were pervasive and were overlain (as preserved on the rock) by the well-preserved, fine strands (layer 2). According to this view the apparent patches are the only parts of the underlying tissue (layer 1) that can be viewed through tears ('windows') in layer 2. While this must remain a

Figure 3. (a) Diagrammatic interpretation of the preservation of the strips of tissue (upper layer) in near parallel rows of GLAHM V1180a. The top arrows in the NE-SW direction show both the direction of contraction of the fibres and creasing and the orientation of the 'stubs' of fibres. The bottom arrows show the NW-SE orientation of the long strands of fibres. (b) Diagrammatic transverse section of the two layers of skin fibres showing how bacterial degradation of layer 1 may have occurred.

possibility there are reservations. First, this would place layer 2 above layer 1 (as preserved). Thus, the thin fibres of layer 2 would lie internal (in terms of the animal) to the 'pervasive' layer 1. Hence, it would be difficult to explain internal tears. Admittedly a few strips of tissue (layer 1) show slight distortion or anastomosing of the fibres around them. This may have occurred during the decay of layer 1 as it contracted and pulled on layer 2 in the initial creasing or, very probably, during pressing of layer 2 against the strips of tissue. Furthermore, the darker appearance of layer 2 is a good indication as to its relative position. The apparent blackness results from the whitish fibres (layer 2), with less skin tissue preserved between them in places, lying on the dark rock matrix (the latter perhaps covered by a black film). Where these fibres are better preserved (figure 2a, semicircled and bottom right), obscuring the matrix, the colour is similar to that of the strips. Layer 1 also appears lighter because it lies against fibres rather than the dark matrix. It is also noteworthy that there are areas in which longer than usual strands of fibres extend from the patches or strips of tissue (layer 1, arrows) which do not suggest a window (figure 2a). In my view it is unlikely that layer 2 was above layer 1 with windows to the latter.

The possible reasons for creasing or folding of the skin are manifold. In addition to collagen, elastin fibres arranged within a collagen framework are present in

skin. Veronda & Westman (1970) showed that the resting strain of cat skin corresponds to an extension of $l=1.25$, well within the low modulus, elastin-dominated region as seen in the curve in their graph (their fig. 4.12). This apparent pre-stressing means that the skin is continually under tension and that the fibres are laid down while under tension. The fibres will remain flat as long as they are under tension, but will fold when the tension is removed (Wainwright *et al.* 1976). It seems reasonable to infer from such studies that creasing may occur with post-mortem damage to the skin and be preserved in fossils such as GLAHM V1180a.

It is interesting that only layer 1 of the two closely associated layers of the skin had creased. This may give some idea of the way in which at least some of the layers of fibres were arranged in ichthyosaurs. For instance, in the earthworm, the collagen fibres show a crossed laminar pattern (Vincent *et al.* 1991), i.e. overlapping of the fibres of the different layers which makes creasing of individual layers less likely. In contrast, in GLAHM V1180a the absence of cross-laminated fibres may account for the creasing of layer 1 without it affecting layer 2. In sharks, Motta (1977) similarly found that, in the skin, crossover fibres were absent in a number of layers of fibres but present in some layers. In the latter case the fibres were more difficult to tease apart. The freedom allowing the sliding of the fibres of one layer over another may have some functional advantage, e.g. coping with varying stresses on the skin during locomotion. For instance, during tensile testing in *Carcharias laticaudus* the fibres of adjacent lamellae were found to slide past one another to orient towards the stress axis (Naresh *et al.* 1997).

(b) Skin fibre orientations

Fibre systems in skin often comprise a random three-dimensional feltwork (Wainwright *et al.* 1976). Although preferred directions of extension may occur in different parts of the body, in many cases the fibres are organized in distinct layers in opposing directions. In living reptiles, masses of collagenous fibres are present in the skin in the corium of the dermis (Harris 1963, fig. 6), less densely packed than in GLAHM V1180a and with a generally random orientation. However, the absence of any great similarity between the arrangement of fibres in living reptiles and that of ichthyosaurs may not be particularly relevant when considering the ubiquitous nature and patterns of collagenous fibres in the skin of various animals. Rather, function appears to be the dominant factor in determining fibre orientation and distribution. Consequently, the fibre arrangement in the ichthyosaur GLAHM V1180a is considered from a functional perspective, principally with respect to the marine environment, namely in protection and/or locomotion.

Perhaps the closest analogy of a meshwork of fibres is in the helically wound fibres in sharks. In sharks the fibres are wound round the animal's body in alternating layers describing right- and left-handed helices and forming a special meshwork. Because of insufficient preservation and the area in which the fibres occur in GLAHM V1180a, namely the posterior lower jaws, it is not possible to say whether or not the fibres were helically arranged in ichthyosaurs although the condition cannot be precluded. For the present, the fibres are simply considered as

forming an orthogonal net (in this respect similar to, for example, those in sharks and tuna).

The lower angle of fibre orientation in GLAHM V1180a compared, for example, to that in sharks (e.g. Motta 1977; Wainwright *et al.* 1978) may have resulted from poor preservation or may vary depending on the particular location of the fibres in the body (cf. *ca.* 60° in the central area of the body in SMF 457; see below) as in sharks (e.g. Motta 1977) and tuna (Hebrank & Hebrank 1986).

D. M. Martill (referee's report) questioned the 'cross-ply' orientation of the fibres based on his view that, unlike layer 1, layer 2 is preserved as black fibres. He therefore proposed two preservational types representing, for example, skin and muscle. However, we have already seen above that there are no fundamental differences in the preservational types in the two layers. Besides, the fibre thickness and density of layers 1 and 2 are so similar that it would seem too much of a coincidence for them to represent two different tissue types such as muscle and skin.

That the fibres are collagenous can reasonably be conjectured by analogy—the orthogonal meshwork is similar to that of sharks and tuna where they are collagenous. The fibres are also identical in SMF 457 where they are certainly part of the integument (Lingham-Soliar 2000) and not the muscles.

(c) *Comparison with preserved fibres in other marine vertebrates and other ichthyosaurs*

Fibres preserved in the integuments of other ichthyosaurs have been mentioned by Broili (1942) and Wiman (1946), i.e. *Stenopterygius* specimens SMF 457 and PMU (Paleontological Museum, Uppsala) 435, respectively. The fibres described in both these specimens are very thick at *ca.* 0.5 mm (4–5 strands cm^{-1}). Recent examination (Lingham-Soliar 2000) has shown that there are two further types of fibre in SMF 457 which are *ca.* 0.2 mm thick (*ca.* 15 strands cm^{-1}) and 0.1 mm thick (40–45 strands cm^{-1}), the latter virtually identical to those of GLAHM V1180a. The preservation of the fine fibres of SMF 457 (*ca.* 0.1 mm thick) is restricted to a very small area on the mid-dorsolateral surface. Thus, the preservation of fibres in a relatively large area in GLAHM V1180a and in two superimposed layers showing an orthogonal meshwork in ichthyosaurs for the first time emphasize the significance of this specimen.

The discovery of such closely similar skin fibres in GLAHM V1180a and SMF 457 in very different parts of the ichthyosaur body suggests that these fine fibres (*ca.* 0.1 mm thick) may have been associated with virtually the entire surface of the animal (Lingham-Soliar 2000).

The fibres described in GLAHM V1180a represent the thinnest (*ca.* 0.10 mm) so far observed in an ichthyosaur (equal to that of SMF 457) and belong to the outermost layer judging by the layers of different fibre types observed in SMF 457. How does the fibre thickness compare with those of other aquatic vertebrates? In the teleost, the Norfolk spot (*Leiostomas xanthurus*, *ca.* 20 cm long and skin thickness 0.220–0.300 mm), the fibre thickness ranges from 0.004 to 0.01 mm while in skipjack tuna (*Katsuwonus pelamis*, *ca.* 50 cm long and skin thickness 0.280–0.350 mm) it is between 0.02 and 0.08 mm thick (Hebrank & Hebrank 1986). Naresh *et al.* (1997) showed

that, in adults of the shark *C. laticaudas* (size of animal not known), the fibre thickness ranges from 0.049 to 0.075 mm. However, to my knowledge, the thickest fibres recorded in extant aquatic vertebrates are found in the Brazilian catfish (*Pseudoplatystoma fasciatum*, *ca.* 55 cm long and skin thickness 0.6 mm; Junqueira *et al.* 1983) which range between *ca.* 0.06 and 0.09 mm (calculated from the authors' figures). The fibre thickness and plaiting have produced a very strong skin, so much so that Junqueira *et al.* (1983) recommended it to the leather industry. The thickest fibres so far recorded in aquatic vertebrates match the finest fibres in GLAHM V1180a and SMF 457. Add to this the thick fibres of ichthyosaurs, e.g. SMF 457 and we have an animal with a highly developed and strong fibrous structure of the outer integument.

(d) *Functional significance of fibre orientation*

The helical fibre systems in the skins of many animals have been discussed in a number of studies (Wainwright *et al.* 1976, 1978; Motta 1977; Alexander 1987; Vincent 1990) and the principles of an orthogonal or lattice web were excellently discussed by Gordon (1978, pp. 250–253). Among vertebrates such as sharks, one function of an orthogonal arrangement of the fibres is thought to be the stabilization of the straight position of the animal (Alexander 1987). The lattice arrangement of the fibres also affords the extensibility necessary for tight bends of the animal without compression of the tube-like body. During contraction of the muscles on one side they shorten and increase in cross-sectional area and girth. The changes in fibre angle imposed by the muscle causes the skin to remain taut in containing the muscle volume and avoid wrinkling or loss of tension on the concave side of the fish (Wainwright *et al.* 1978). In notable examples such as dolphins (Fish & Hui 1991; Fish 1993) and tuna (Hebrank & Hebrank 1986) the smooth body surface is considered to aid in the general streamlining properties that counteract fluid drag.

Because of the restricted areas of preservation in all mentioned ichthyosaur specimens with fibres, there is no evidence that the fibres were helically wound. An alternative possibility is that they may have been attached at the dorsal surface of the animal to horizontal strands as, for example, in SMF 457 (fibres of intermediate thickness of 0.2 mm) (Lingham-Soliar 2000). Motta (1977) also noted that not all fibres in sharks were helically wound but that there was a dorsal attachment for some. This is thought to be the means of attachment in cetaceans (Gambarian & Sukhanov 1986). Whatever the attachment of the thin fibres in GLAHM V1180a, it is reasonable to conclude that dense layers of apparently pre-stressed, orthogonally arranged fibres would have helped contain the muscle volume changes in ichthyosaurs and prevented wrinkling of the skin, comparable to the role in tuna and sharks where they maintain a smooth and stiff hydrodynamic surface. An especially tough skin would also have performed a protective function (emphasized in addition by the layers of thicker fibres in SMF 457 and PMU R435 mentioned above). However, it would be premature to consider the skin of *Stenopterygius* as an external tendon as in sharks (Wainwright *et al.* 1978).

This is the first record of fibres in the head of an ichthyosaur. Their presence is reasonable in terms of

hydrodynamic streamlining, since the head is the first line of resistance to water and a smooth surface would be beneficial (cf. the smooth heads of many whales and dolphins).

Previous workers (e.g. Lighthill 1975; Taylor 1987; Massare 1988; Alexander 1989; McGowan 1992) have considerably advanced our ideas of ichthyosaur swimming potential, principally from functional interpretations based on body and tail shape. The present paper presents rare anatomical evidence that may extend information supporting the concept of ichthyosaurs as hydrodynamically streamlined animals and as fast swimmers.

I am much indebted to Dr Neil Clark of the Hunterian Museum, Glasgow for his considerable help regarding specimen GLAHM V1180a and for his excellent photographs. I am particularly grateful for the highly constructive comments from two unnamed referees and encouragement in publication. Thanks are due to Dr David Martill (University of Portsmouth), a third referee for useful comments and Professor Wolf-Ernst Reif and Dr Axel Hungerbühler (University of Tübingen) who provided valuable discussions on ichthyosaurs generally during successive Royal Society postdoctoral fellowships to the University of Tübingen, Germany.

REFERENCES

- Alexander, R. M. 1987 Bending of cylindrical animals with helical fibres in their skin or cuticle. *J. Theor. Biol.* **124**, 97–110.
- Alexander, R. M. 1989 *Dynamics of dinosaurs and other extinct giants*. New York: Columbia University Press.
- Allison, P. A. 1988a Phosphatized soft-bodied squids from the Jurassic Oxford Clay. *Lethaia* **21**, 403–410.
- Allison, P. A. 1988b Konservat-Lagerstätten: cause and classification. *Paleobiology* **14**, 331–334.
- Allison, P. A. & Briggs, D. E. G. 1991 The taphonomy of soft bodied animals. In *The process of fossilization* (ed. S. K. Donovan), pp. 120–140. London: Belhaven Press.
- Broili, F. 1942 Vesfestigungen im Integument der Ichthyosaurier. *Sher. Bayer. Akad. Wiss. Math.-nat.* **1942**, 37–52.
- Buckland, W. 1836 *Geology and mineralogy (Bridgewater Treatise)*. London.
- Burne, R. H. 1952 *Handbook of R. H. Burne's cetacean dissections*. London: Trustees of the British Museum.
- Delair, J. B. 1966 Unusual preservation of fibrous elements in an ichthyosaur skull. *Nature* **212**, 575–576.
- Fish, F. 1993 Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). *J. Exp. Biol.* **185**, 179–193.
- Fish, F. & Hui, C. A. 1991 Dolphin swimming—a review. *Mamm. Rev.* **21**, 181–195.
- Gabbott, S. E. 1998 Taphonomy of the Ordovician Soom Shale lagerstätte; an example of soft tissue preservation in clay minerals. *Palaeontology* **41**, 631–668.
- Gambarian, P. P. & Sukhanov, V. B. 1986 Structure, functions and adaptations of the skeletal musculature in lamantine. In *Lamantine. Morphological adaptations* (ed. V. E. Sokolov), pp. 188–305. Moscow: Nauka.
- Gordon, J. E. 1978 *Structures*. UK: Penguin Books.
- Halstead, L. B. 1974 *Vertebrate hard tissue*. London and Winchester, UK: Wykeham Publication.
- Harris, V. A. 1963 *The anatomy of the rainbow lizard Agama agama (L)*. London: Hutchinson & Co. Ltd.
- Hebrank, M. R. & Hebrank, J. H. 1986 The mechanics of fish skin: lack of an 'external tendon' role in two teleosts. *Biol. Bull.* **171**, 236–247.
- Junqueira, C. C. U., Joazeira, P. P., Montes, G. S., Menezes, N. & Pereira-Filho, M. 1983 The collagen fiber architecture of Brazilian naked catfish fish. *Brazil. J. Med. Biol. Res.* **16**, 313–316.
- Lighthill, J. 1975 *Mathematical biofluid dynamics*. Philadelphia, PA: Society of Industrial and Applied Mathematics.
- Lingham-Soliar, T. 2000 The ichthyosaur integument: a means for a stiff, smooth skin. *Lethaia*. (Submitted.)
- Lingham-Soliar, T. & Reif, W.-E. 1998 Taphonomic evidence for fast tuna-like swimming in Jurassic and Cretaceous ichthyosaurs. *N. J. Geol. Paläont. Abh.* **207**, 171–183.
- McGowan, C. 1973 The cranial morphology of the Lower Liassic latipinnate ichthyosaurs of England. *Bull. Br. Mus. (Nat. Hist.) Geol.* **24**, 1–109.
- McGowan, C. 1992 The ichthyosaur tail: sharks do not provide an appropriate analogue. *Palaeontology* **35**, 555–570.
- Martill, D. M. 1987 Ichthyosaurs with soft tissue: additional comments. *Trans. Leicester Litt. Phil. Soc.* **81**, 35–45.
- Martill, D. M. 1993 Soupy substrates: a medium for the exceptional preservation of ichthyosaurs of the Posidonia shale (Lower Jurassic) of Germany. *Kaupia* **2**, 77–97.
- Martill, D. M. 1995 An ichthyosaur with preserved soft tissue from the Sinemurian of southern England. *Palaeontology* **38**, 897–903.
- Massare, J. A. 1988 Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. *Paleobiology* **14**, 187–205.
- Motta, P. J. 1977 Anatomy and functional morphology of dermal collagen fibres in sharks. *Copeia* **1977**, 454–464.
- Naresh, M. D., Arumugam, V. & Sanjeevi, R. 1997 Mechanical behaviour of shark skin. *J. Biosci.* **22**, 431–437.
- Taylor, M. A. 1987 Reinterpretation of ichthyosaur swimming and buoyancy. *Palaeontology* **30**, 531–535.
- Veronda, D. R. & Westman, R. A. 1970 Finite deformations of skin. *J. Biomech.* **3**, 111–124.
- Vincent, J. F. V. 1990 *Structural biomaterials*, revised edn. Princeton University Press.
- Vincent, J. F. V., Jeronimidis, G., Topping, B. H. V. & Khan, A. I. 1991 The mechanical design of skin—towards the development of new materials. *Nat. Struct. Principl. Strat. Models Architect.* **6**, 165–170.
- Wainwright, S. A., Biggs, W. D., Currey, J. D. & Gosline, J. M. 1976 *Mechanical design in organisms*. London: Edward Arnold.
- Wainwright, S. A., Vosburgh, F. & Hebrank, J. H. 1978 Shark skin: function in locomotion. *Science* **202**, 747–749.
- Weigelt, J. 1989 *Recent vertebrate carcasses and their paleobiological implications* (German edn, originally published 1927). University of Chicago Press.
- Wild, R. 1990 Holzmaden. In *Palaeobiology* (ed. D. E. G. Briggs & P. Crowther), pp. 282–285. Oxford, UK: Blackwell Scientific Publications.
- Wiman, C. 1946 Über Ichthyosaurier und Wale. *Senckenbergiana* **27**, 1–11.

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.