

Growth, age and size of the Jurassic pachycormid *Leedsichthys problematicus* (Osteichthyes: Actinopterygii)

Jeff LISTON, Michael G. NEWBREY, Thomas James CHALLANDS
and Colin E. ADAMS

Abstract

The Jurassic pachycormid osteichthyan *Leedsichthys problematicus* is renowned for having been able to achieve prodigious size for a bony fish. Building on work of MARTILL (1986a), a thorough examination of all known material was conducted in order to constrain estimates of the size of this animal and examine its rate of growth. Important specimens of *Leedsichthys* are described for the first time. The histology of *Leedsichthys* is reviewed, and the presence of growth annuli is used to establish ages for five specimens. Age and growth data were obtained from gill rakers (n=4) and lepidotrichia (n=2). Lepidotrichia show upward curvilinear growth profiles and ages ranging from 21 to 40 annuli, which are assumed to represent years. Both growth profiles start at a small size (0.26 and 0.33 mm radial distance), which is assumed to represent age 1. However, annuli can be lost near the margins of the elements. Gill rakers exhibit a sigmoidal growth profile. Age of gill rakers was estimated by adjusting the alignment of the inflection points of the growth profiles thereby giving adjusted ages. Gill rakers ranged in age from 19–38 annuli, but all show evidence of reabsorption of annuli near the focal points and at the margins of most elements. Sizes for the five individuals range from 8.0–16.5 m for ages of 19–40 years. Growth rate (0.01–0.05 K) was relatively slow as expected for a large, long-lived fish. At age 1, individuals were 1.6 m in length. Estimates for the length of *L. problematicus* compare well with published lengths of other large suspension feeders such as those for basking and whale sharks.

Introduction

Dutch naturalist Thonis PHILIPSZOON (Antonie VAN LEEUWENHOEK) was the first to notice in 1684 that there was a connection between the age of fish and the number of rings on their scales (specifically, on an eel – VAN LEEUWENHOEK 1685). The Swedish clergyman Hans HEDERSTRÖM (1759) first recognised growth marks in the bones of bony fishes (osteichthyans). Since then, with increasing levels of support from the fisheries industry, researchers have recorded their occurrence in, for example, cleithra (CASSELMAN 1974, BEAMISH & MCFARLANE 1987, CASSELMAN 1996), opercula (FROST & KIPLING 1959, NIKOLSKY 1963), vertebral centra (WELDEN et al. 1987, NEWBREY & WILSON 2005), fin rays (BEAMISH 1981, BURTON et al. 1999), and fin spines (MCFARLANE & BEAMISH 1987), all of which (with the exception of vertebral centra) are certainly present in the pachycormid *Leedsichthys problematicus* (Osteichthyes: Actinopterygii). The fisheries industry has focussed on analysis of otoliths (MESSIEH et al. 1987) and scales. However, otoliths and scales have many drawbacks and problems (CARLANDER 1987, BEAMISH & MCFARLANE 1987, RICE 1987, LENTSCH & GRIFFITH 1987, O'GORMAN et al. 1987), particularly in comparison with other bones (CASTANET et al. 1993). Workers on fossil fishes still use scales, branchiostegal rays (MICKLICH 2002), and otoliths (e.g. REICHENBACHER & SIENKNECHT 2001), but this is precluded in *Leedsichthys* as none of these components has been identified. In *Leedsichthys*, the marks of skeletal growth occur in the splanchnocranium and the appendicular skeleton.

Leedsichthys has been recognised as an unusually large bony fish since it was first described (WOODWARD 1889) and has recently been recognized as the acme of a dynasty of Mesozoic osteichthyan suspension feeders (FRIEDMAN et al. 2010). It is known from the Callovian of England (Peterborough, Christian Malford), France (Normandie), northern Germany (Wiehengebirge), the Oxfordian of Chile (east of Antofagasta) and the Kimmeridgian of France (Cap de la Hève) (LISTON 2008b, 2010). Its osteology has remained poorly known, owing to fragmentary remains and a sparsely ossified skeleton giving it low preservational potential. Nevertheless, *Leedsichthys problematicus* has been claimed to be the largest bony fish to ever exist (MARTILL 1986a). However, it is important to be cautious of inadvertently creating giants of mythical proportions (FORTELIUS & KAPPELMAN 1993), where the slightest misidentification of scant fossil remains can result in significant differences of estimated size in extinct animals (e. g., LISTON 2004a). As a large suspension-feeding fish (LISTON 2004b, ALEXANDER 1998), *Leedsichthys* represents a significant ecological indicator for the levels of productivity in the Oxford Clay sea. In an attempt to quantify this productivity, a series of scaling exercises were carried out (building on the efforts of MARTILL 1986a), using a variety of remains of *Leedsichthys* and other members of the family Pachycormidae to estimate likely lengths of this fish. In the absence of a complete specimen which can be measured from the tip of its snout to the base of its caudal fin, it is still possible to estimate the size of *Leedsichthys problematicus* by scaling individual elements from other fishes preferably of a similar length and from a closely related or at least an intrafamilial taxon, to constrain any allometric distortions.

Skeletal growth marks are produced by internal rhythms, which may become synchronized with and/or reinforced by seasonal environmental cycles, but they are not in themselves indicators of seasonality (CASTANET et al. 1993). Such marks have been well known for some time in the Callovian (Middle Jurassic) Oxford Clay, with crocodylians (*Steneosaurus* and *Metrirorhynchus*) recording such marks clearly in their teeth (LISTON 2007). The presence of apparent growth increments on some of the bones of *Leedsichthys* was noted, and subsequent work (LISTON et al. 2005) distinguished between different types of growth bands in different bones of this taxon, revealing the presence of annuli in cross-sections of gill rakers and lepidotrichia. A histological analysis of bony remains of *Leedsichthys* was used to estimate the age and growth of the specimens.

Material and methods

Institutional abbreviations

Ba, Staatliches Museum für Mineralogie und Geologie zu Dresden, Dresden, Germany; **GLAHM**, Hunterian Museum, University of Glasgow, Glasgow, Scotland; **JM**, Jura-Museum, Eichstätt, Germany; **NHM**, Natural History Museum, London, England; **PETMG**, Peterborough Museum, Peterborough, Cambridgeshire, England; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **WMfN**, Westfälisches Museum für Naturkunde, Münster, Germany.

Material examined

The following taxa were studied:

Asthenocormus titanius: Ba J 2344; JM SoS 542 (neotype); JM SoS 3556.

Martillichthys renwickae: NHM P.61563 (holotype).

Leedsichthys problematicus: NHM P.6921 (holotype); NHM P.10000 ('Tail' specimen); NHM P.10156 ('Gill Basket' specimen); GLAHM P.11823, GLAHM 109519 ('Wallücke' specimen); GLAHM V3363 ('Big Meg'); PETMG F174 ('Ariston'); WMfN P20238 ('Wallücke' specimen).

Saurostomus: specimen SMNS St56982.

Pachycormid, unidentified: SMNS St12576.

Such skeletal elements were selected, which could be used for size ranking, scaling, or sampled for growth ring analysis. The majority of the remains of *Leedsichthys* consists of fragments of dermal bones, gill rakers and ceratobranchials. However, some remains contain more useful comparative elements for estimating size; of these, three specimens preserve discrete sections of the body in an apparently in vivo fashion: NHM P.10000 (the 'Tail' specimen collected by Alfred Nicholson LEEDS in 1898, LISTON & NOË 2004; NHM P.10156 (the 'Gill Basket' specimen, collected by A. N. LEEDS in 1905); PETMG F174 ('Ariston', the specimen collected by LISTON, DAWN, MARTILL and others in 2002–2003, LISTON 2006). 'Ariston' (PETMG F174) contains a complete and intact pectoral fin. Although not yet fully prepared, field data for this specimen provide valuable insights into size that aid understanding of the pectoral fragment associated with the 'Tail' specimen (NHM P.10000).

Measurements

Estimating the standard length of *Leedsichthys*

Taxa used to estimate relative size: Trying to estimate the standard length (SL, sensu HOLČIK et al. 1989) from such isolated components is difficult, and it is hoped that the task will be rendered easier when PETMG F174 ('Ariston') is fully collected and prepared out of its matrix. In the interim, it is appropriate to make comparisons with the above described partial remains, and relate them to other large pachycormids for indications of how these remains might scale to the SL of a specimen of *Leedsichthys problematicus*. In this regard, MARTILL (1986a) used a 2 m long pachycormid (subsequently described as *Martillichthys renwickae* LISTON 2008a) that had recently been retrieved from the Oxford Clay. This was in spite of the cautionary comments by PATTERSON (letter to MARTILL, 11/10/1983) on the unusual braincase length relative to its body length; however, MARTILL (1991) himself later acknowledged its "disproportionately small" tail for the length of its body. The largest pachycormid fishes belong to the genera *Martillichthys* (2.3 m SL, NHM P.61563) and *Asthenocormus* (a juvenile 1.18 m SL [Ba J 2344] and adult specimens of 1.9–2.1 m SL [JM SoS 542 and JM SoS 3556 respectively]) known from the Solnhofen Limestone (Tithonian) of Germany (LISTON 2008a). Specimens of these two genera will not, however, be used for scaling as few bone morphologies of *L. problematicus* can be recognized in specimens of these taxa. In contrast, *Saurostomus esocinus*, a taxon from the older Toarcian Holzmaden shale of Germany, for which specimens of as much as 1.7 m SL are known (e.g. SMNS St.56982), does have elements with similar morphologies when compared to those of *L. problematicus* (LISTON 2004b, WOODWARD 1916). As such, this taxon will primarily be the one used for comparison and scaling purposes.

Allometry and estimation of size

Leedsichthys problematicus has been concluded to be a suspension feeder based on the large size of many of the remains, the complete absence of any teeth, and the presence of highly developed gill rakers (WOODWARD 1890, DIAMOND 1985, MACNEILL & BRANDT 1990, WEBB & BUFFRENIL 1990, ALEXANDER 1998, BATTY & DOMENICI 2000, WEBB & GERSTNER 2000). It is likely that specialist adaptations took place within the skull to facilitate this lifestyle. SANDERSON & WASSERSUG (1990) noted a tendency in large, ram suspension feeders such as baleen whales and the three large suspension-feeding sharks (*Megachasma*, *Rhincodon*, *Cetorhinus*) to have skull lengths that were 25–28 % of their SL. In addition, EMERSON & BRAMBLE (1993) have noted the marked negative allometry of skull elements with respect to body size even among very closely related taxa.

With regard to *Leedsichthys*, it is necessary to eschew such components in any exercise of size estimation as unreliable data sources for scaling. For example, MARTILL (1986a) estimated two disparate lengths of *L. problematicus* from the same specimen (NHM P.10156: 13.5–27.6 m SL), depending on whether one scaled from the length of the hyomandibula or the width of the gill basket, respectively. It should, however, be noted that it is unclear which specific element MARTILL was scaling from because no hyomandibula is apparent in the specimen used (NHM P.61563) and MARTILL later (1988) figured the hyomandibula of *Leedsichthys* as a ceratohyal. Therefore, it is assumed that postcranial elements will produce a more realistic estimated length. However, it is difficult to find elements that are identifiable both in partial disarticulated remains of *Leedsichthys* and in intact well-preserved pachycormids.

This is a particular problem for the 'Gill Basket' specimen (NHM P.10156), which features little postcranial material (only fragments of pectoral and other fin rays). However, it does feature one of the more ubiquitous and robust elements within the skeleton of *L. problematicus*, the hyomandibula. The length of this bone, although perhaps not reliable as a direct reference for scaling, should give an indication of relative size between different specimens.

Hypobranchials and ceratobranchials were also considered for use in this exercise, due to their reasonably common occurrence in specimens of *Leedsichthys*, but there were two problems that excluded them. Firstly, they had been subjected to variable degrees of crushing; therefore, horizontal distances were difficult to measure in a uniform way for all specimens. This introduced a significant amount of error. The second problem is that no specimen exists for which all the hypobranchials are known; therefore, the expected range within the series of an individual is difficult to determine. Similarly, the ceratobranchial series is only known in full for one individual (NHM P.10156), but the supporting clay would need to be more fully excavated before widths of these tapering elements could be confidently measured. This last element of error meant that neither of these branchial series could be used to rank size in specimens, despite their common occurrence.

The preopercle and ceratohyal were both selected for use. Depth of the ceratohyal was used instead of its length, because the superior and inferior surfaces are more robust and well defined than the fragile and frequently incomplete proximal and distal ends. However, only partial remains of the left ceratohyal of the 'Gill Basket' specimen are preserved, covering the first and second left hypobranchial, so that only a minimum (rather than an absolute) value of 84 mm could be ascertained for its depth, with a minimum estimate of about 160 mm depth based on comparison of the orientation of surface striae with those of other specimens. If the striae extended farther over the surface of the bones, this ceratohyal could have been up to 230 mm deep.

Comparison of skull elements across the sample group indicates that specimens are, in decreasing order of relative size (see Table 1): ‘Gill Basket’, holotype, ‘Big Meg’, ‘Tail’, ‘Ariston’ and subadult (NHM P.11823).

Specimen preparation

Gill rakers were sampled from the ‘Ariston’, ‘Tail’, holotype, and ‘Gill Basket’ specimens. Lepidotrichial and other unidentifiable meristic fragments were also sampled, to compare results with the counts obtained from the gill rakers, and as a substitute element for ‘Big Meg’, which lacks gill rakers. Meristic is used in the sense of LINDSEY (1988) to refer to serially repeated skeletal structures. It is used here as a sampling category distinct from gill rakers and lepidotrichia, to refer to internal, elongate (i.e., not scales, scutes or vertebrae) elements, possibly fragments of ribs or fin supports. It was difficult to establish a rigorously consistent location along a gill raker for making a transverse section, as gill rakers are rarely found complete. Preference was given to the section presenting annuli with greatest clarity, rather than from a consistent position along the length of the raker. Sections from both types of bones were mounted as polished sections for microscopic examination, photography and analysis using Image J 1.33u (2004) software. Elements for growth-ring analysis were mounted in petropoxy resin in aluminium rings, and left to cure in an oven at 80°C for twelve hours. The mount was then ground down to reveal a flat surface, using incrementally finer grinding papers of P120, P800, P1200 and P2500. The samples were then cleaned in iso-propynol in an ultrasonic bath for five minutes (CHALLANDS 2003), prior to photography using a halogen point-source light. Polished mounts were viewed under a binocular microscope in reflected light. The difference in hardness of void-filling calcite (hardness 3) and fossil bone (hydroxyapatite, hardness 5) produces relief between these two phases when a specimen is highly polished. When viewed in reflected light, gradations between regions of dense bone and less-dense bone also produce relief when polished. This emphasises bone structure, in particular growth rings and differences between cortical bone and cancellous bone. Maximum reflectivity and greatest contrast between areas of different relief were achieved by positioning the reflected light source above the specimen (at a high angle of incidence). Alternatively, a brighter light source may be positioned at a lower angle of incidence closer to the specimen. Images were taken with a 3.2 megapixel Olympus CAMEDIA C-310ZOOM camera using the macrozoom function.

Description of specimens

NHM P.10000 – the ‘Tail’ specimen

This specimen consists of the tail, a fragment of a pectoral fin, and a variety of gill rakers and skull elements. The tail itself consists solely of fin-rays, with no preural haemal or neural arch elements. Figure 1 shows the tail mounted on the painted background that was made for its public display at the NHM (LISTON & NOË 2004), adding some of the missing elements, including the smaller distal extremities of the branching rays (LEEDS 1956). Similarly, the inter-lobe space was included in the background, with the hypural plate depicted. The area to the rear would presumably have been covered by the longitudinal hypochordal muscle (WINTERBOTTOM 1974). The fin consists of two discrete lobes, but the proper orientation is not apparent. In the following description, the terms ‘upper lobe’ and ‘lower lobe’ will be used to distinguish between the lobes as historically displayed, rather than indicating an anatomical interpretation of the components as dorsal or ventral elements.

The maximum width (perpendicular to the caudal rays [sensu HUBBS & LAGLER 1964]) of the upper and lower lobes is 550 mm and 500 mm respectively, and their lengths are 1500 mm and 1460 mm. The

lobes are mounted juxtaposed to each other in a fashion that approximates the position in which they were found (this interpretation is based upon a sketch made by LEEDS during the period of excavation; see LISTON & NOË 2004). As such, it is important to note the distances that these lobes would occupy as part of a functioning caudal fin; the horizontal extents of the upper and lower lobes are 1020 mm and 1090 mm respectively. The vertical extent

Table 1.

Ranking of dimensions of three skull bones across six specimens of *Leedsichthys problematicus*.

	Ceratohyal dimensions	Length of hyomandibula	Preopercle dimensions	Rank (1 = largest)
NHM P.11823		530		6
‘Ariston’	100	663	575	5
‘Tail’	125	[> 650 – broken]		4
‘Big Meg’	141		771	3
holotype	152		812	2
‘Gill Basket’	[> 84, 160–230]	687	820	1

of the fin lobes is 1230 mm and 1140 mm. Each lobe is made up of a left and a right half, each consisting of a series of bifurcating non-segmented rays or lepidotrichia. The lack of segmentation is a distinctive feature in the caudal fins of some pachycormids (e.g., the Tithonian *Asthenocormus*, a Toarcian pachycormid specimen [SMNS ST12576], and *Martillichthys renwickae* [NHM P.61563], the Callovian pachycormid from the Oxford Clay). These lepidotrichia lie in clusters or units that may be the result of a preservational or excavational artefact rather than a direct reflection of the structure as it was in life, but they are a convenient way of describing the structure of the tail in five separate components: anterior section, mid-section I, mid-section II, mid-section III and posterior section (Fig. 1). The two lobes are extremely similar (LAMBERS 1992, ARRATIA & LAMBERS 1996) and only the lower lobe is described in detail.

The adjacent rays are clearly fused together antero-ventrally and postero-dorsally, when viewed from the subcircular (<5 mm diameter) proximal ends of the lepidotrichia. In life, these would have been covered anteriorly by the ventral and dorsal flexors, and posteriorly by the longitudinal hypochordal muscles (WINTERBOTTOM 1974). These fused rays give the appearance that they lay six deep as a stack of flattened structures, but there are only two sides (left and right), with rays forming a 'pseudostratified' effect when they overlie each other. Initially the rays, 38 in number, are 15 mm wide with a fasciculated appearance of striations, as though many smaller rays have become fused proximally. Distally, they thicken and separate from each other to become discrete rays. In the anterior component (rays 1–6, Fig. 1), after the first 230 mm, visible units are 10 mm wide, with fewer striations and a subcircular cross-sectional silhouette. This anterior component is just over a meter in length, with no apparent bifurcations preserved. Mid-section I (rays 7–11) is about a meter in length. Rays 7–11 lose their fasciculated appearance at around 320 mm and bifurcate at 840–940 mm. There is a callus growth present on one of the rays. In mid-section II (about 1560 mm long), the rays are often laterally paired, with a 'knitting needle' thickness (LEEDS 1956) at their proximal origin. They lose their fasciculated character at about 215 mm distally, just proximal to a large horizontal mark across the lobe, which is presumably damage caused during excavation. At this

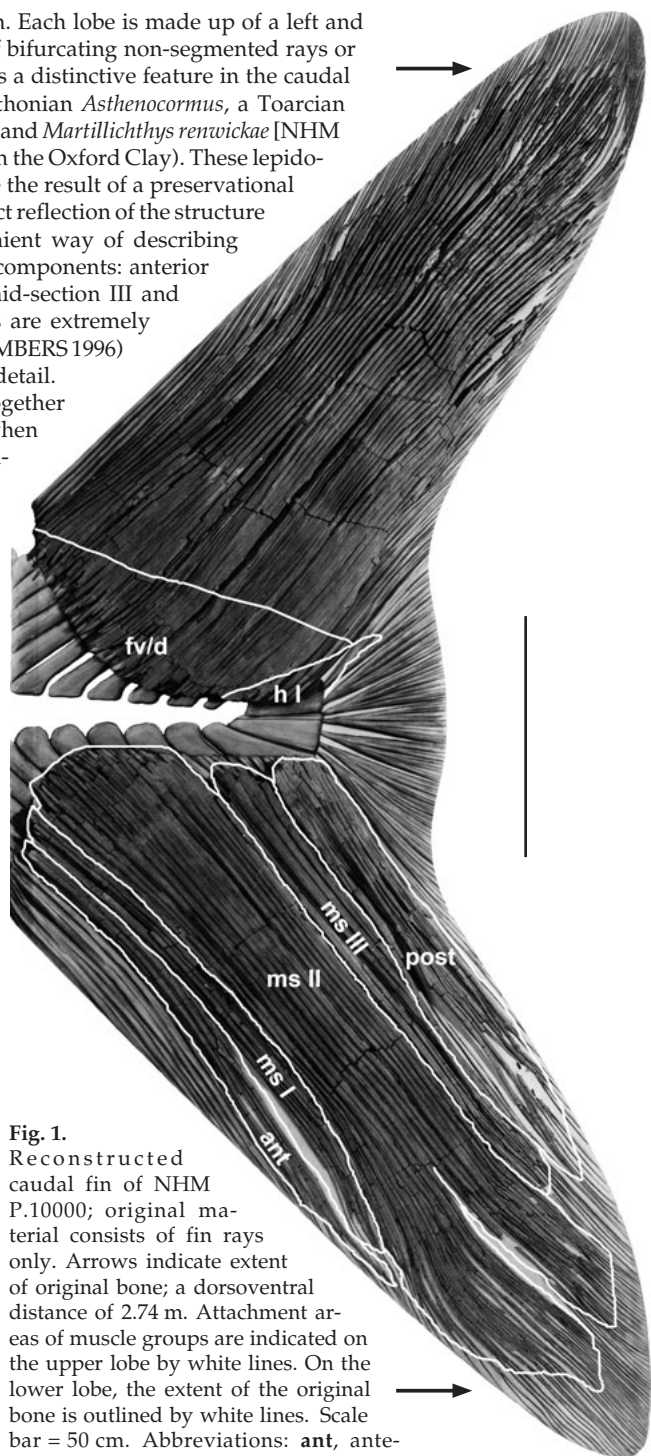


Fig. 1. Reconstructed caudal fin of NHM P.10000; original material consists of fin rays only. Arrows indicate extent of original bone; a dorsoventral distance of 2.74 m. Attachment areas of muscle groups are indicated on the upper lobe by white lines. On the lower lobe, the extent of the original bone is outlined by white lines. Scale bar = 50 cm. Abbreviations: **ant**, anterior-section; **fv/d**, ventral and dorsal flexors; **hl**, hypural (possible site of longitudinal hypochordal muscle); **ms**, mid-section; **post**, posterior-section.

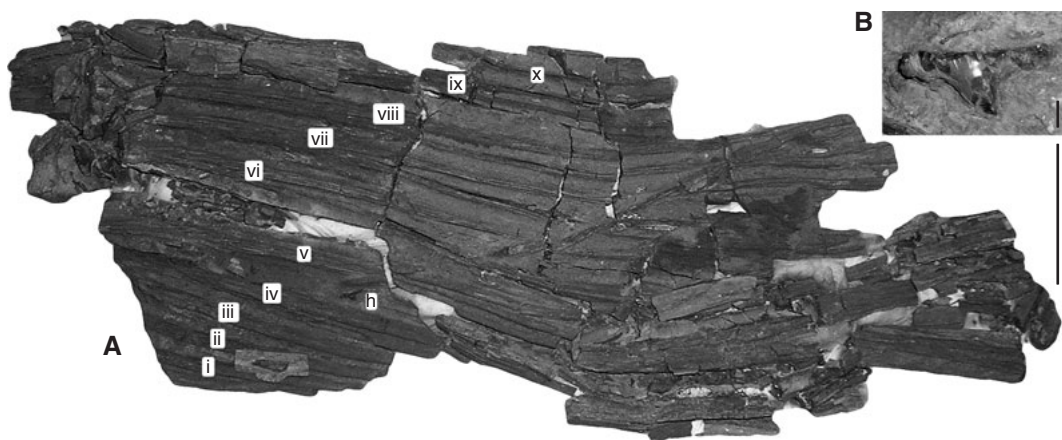


Fig. 2.

Fragment of a pectoral fin of NHM P.10000; 75 cm in length, prior to conservation by M. GUNTER. **A**, proximal end of fin to left of image, leading edge of fin to bottom of image; 10 fin rays i-x are labeled, **h** indicates hybrid tooth. **B**, detail of area between rays vi and v, near base of overlying ray, showing hybrid tooth. Scale bars: A = 10 cm, B = 3 mm.

point, the rays change to a rounded rectangular cross-section proximal to their first bifurcations at around 1100–1260 mm. Distally, each ray bifurcates a total of two or three times. Again, there is a callus growth present on one of the rays. Mid-section III (985 mm long) has a proximal origin with a 20 mm thickness of well-defined fasciculi, which taper over the subsequent 450 mm to only 10 mm in width. These rays then continue for a further 340–370 mm until they bifurcate, and do so only once. There are four callus growths present in this component. In the posterior component (960 mm total length), the overall structure more resembles that of striated sheets of ‘unworked plasticine’ in appearance. These rays are more like triangular planar sheets that taper, over 485 mm, from 30 mm wide to 15 mm wide. The rays lose their striated characteristics distally, at 310 mm. Each of the seven rays has a bone-repair callus at its distal end, and only the first two rays have a single bifurcation distally, at 550–560 mm. The rest of the rays are devoid of such divisions.

The total height of the fin (or the span of its trailing edge) is 2740 mm, and its surface area is 1.745 m². Therefore, the tail has an aspect ratio of 4.32, which is moderately high (VOGEL 1994). Taken in conjunction with its shape and rigidity (absence of segmentation), this has specific implications for the animal’s lifestyle (see Chapter 9 of LISTON 2007).

NHM P.10000 – pectoral fin fragment

Only recognized as part of the ‘Tail’ specimen in recent years, this fragment is 750 mm in length, and 235 mm in maximum width (Fig. 2A). Antero-distally, there is much degradation of the specimen due to clay shrinkage, making observations difficult, but it is clear that this slab does not hold either ray origins or ray terminations. Overall, rays seem parallel until about 400 mm distally, when the rays appear to bend slightly at an angle of about 10 degrees, then continue more posteriorly, presumably indicating a bend in the fin.

At its proximal end, the fin fragment has ten rays, labelled i through x, which extend distally across the slab without segmentation. Bifurcating rays that lack segmentation in both the pectoral and the caudal fins are a key feature of *Leedsichthys*. Again, these rays appear to occur as a double (superior and inferior) layer, although it is conceivable that each simply represents one ray that has bifurcated, around a horizontal plane through the pectoral fin, at a more proximal point to the body than represented on this slab. All rays display rugose striations, with particularly pronounced ornamentation for the first 440 mm of the length of the slab. This ornamentation becomes more evident moving from the leading towards the trailing edge of the pectoral fin fragment, the striations growing in relief until they resemble etched, incised, or elevated laminae by ray nine. This reflects a change from circular rays (in cross-section) to more flattened

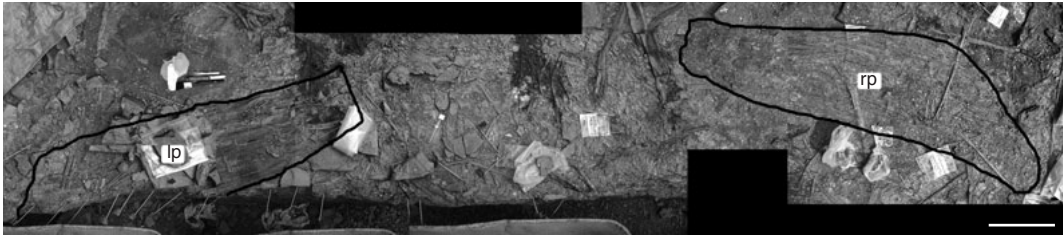


Fig. 3.

Composited image from field excavation of 'Ariston' specimen (PETMG F174), with both pectoral fins outlined, prior to retrieval. The fins are separated from each other by 100.5 cm and outlined in black. Photographs courtesy of D. M. MARTILL on 27 July 2002 in the Star Pit, Whittlesey, but compiled by the author. Scale bar = 20 cm. Abbreviations: **lp**, left pectoral fin; **rp**, right pectoral fin.

rays (initially supero-inferior flattening, then antero-posterior flattening). From the proximal leading edge to the trailing distal point there is a trend towards rays with circular cross-sections. The presumed leading edge of the fin fragment is more robust than the more posterior rays. The first four rays are no longer than 190 mm, and exhibit no trace of bifurcation. After the first 60 mm, ray v bifurcates once before extending for the rest of its 340 mm; at this point, the specimen becomes hard to interpret, due to degradation of the block. There may be a second bifurcation 140 mm farther distally, but a 350 mm long ray straddles the Vth-VIIth rays (and their subsidiary bifurcations), and obscures what might be the point of origin of the ray that emerges on the other side. This ray might also be derived from the underside ray, lying in a slightly twisted position.

Ray vi bifurcates distally at 70, 300, and 500 mm. Ray vii bifurcates at 120 and 350 mm. Ray viii bifurcates at 100 and 410 mm. Ray ix bifurcates at 230 mm. Between rays iv and v, at the base of the overlying ray, is a hybodont tooth (Fig. 2B).

PETMG F174 – 'Ariston' specimen

The pectoral fragment of the 'Tail' specimen (NHM P.10000) can usefully be compared with field data from the recently collected pectoral fins of 'Ariston' (PETMG F174). Both fins were found lying as though disposed *in vivo*, and separated laterally by 1005 mm (Fig. 3). The width of this individual is likely to have been significantly greater than this (given lengths of individual ribs of more than 700 mm), as it is likely that the pectorals were slung below the mid-height level of the body, as would be expected for a pachycormid. The fins are yet to be prepared out from the clay for full examination, and although the leading and trailing edges are apparent, it currently cannot be ascertained whether they are lying upside down or the right way up. They will, however, be regarded as though they are lying the right way up (following the interpretive scheme of MARTILL 1986b). The putative left pectoral fin unfortunately had a structural slip running through it prior to excavation, causing significant damage, and making precise size estimations exceedingly difficult. The putative right pectoral fin does not have this flaw, and has a length of 1363 mm. Through careful examination (prior to encasing in jackets for removal from the field), the equivalent portion to the fragment represented within NHM P.10000 can be identified, and a common traverse line (one that crosses eighteen rays) used. Comparison of the traverse lines of each specimen indicates a fin-width of 278 mm in PETMG F174 and 299 mm in NHM P.10000. If these dimensions reflect overall size differences between the two specimens, then 'Ariston' was the shorter of the two, and suggests that it was possibly a younger individual than NHM P.10000.

NHM P.10156 – 'Gill Basket' specimen

This specimen has been previously described (LISTON 2008a), but a brief description is particularly important here for the purposes of scale, as this specimen has historically been the source of some of the larger estimates of size for this animal (MARTILL 1986a).

The 'Gill Basket' specimen (Fig. 4) consists of several isolated units of clay from a concretionary nodule, containing lengths of fin rays (probably pectoral), a hyomandibula of 870 mm length, and the bulk of a gill basket with some opercular elements (LISTON 2008a: fig. 8). Owing to its preservation



Fig. 4. Ventral aspect of the 155 cm long and 114 cm wide gill basket and 87 cm tall hyomandibula (NHM P.10156). Photograph after one taken on 11 September 1924 by Errol Ivor White. Scale bar = 30 cm. Abbreviations: **cb**, ceratobranchial; **ch**, ceratohyal; **grs**, gill rakers; **hb**, hypobranchial; **hh**, hypohyal; **hm**, hyomandibula; **v**, fused arch.

within a concretionary nodule, all the elements except the hyomandibula and the fin rays can be placed in their original unexcavated position (LISTON 2008a: fig. 8). The gill basket consists of both hypohyals, a left hypobranchial I, both hypobranchial II's, both 810 mm long ceratobranchial I's, both 950 mm long ceratobranchial II's, both 990 mm long ceratobranchial III's, both 940 mm long ceratobranchial IV's, and

the 340 mm long basibranchial IV. Combined with the fused arch V, they produce a gill basket 1140 mm wide and 1545 mm long.

Other material

In order to supplement the above three specimens, which are unusual and important in preserving distinct sections of the animal's body, a series of other specimens is included in the subsequent series of analyses to broaden understanding of age and growth in this taxon.

GLAHM V3363 – ‘Big Meg’ specimen. This represents the most extensive set of remains of *Leedsichthys* to be fully excavated; it was sold to the Hunterian Museum, University of Glasgow in January 1915 (LISTON 2004b, 2006) by A. N. LEEDS (the discoverer of the fish). This specimen features a great diversity of bones among its 904 parts, and is particularly useful in having a series of large skull bones that can be used to establish size-comparative data for a wide range of cranial elements from other specimens, thus permitting determination of a rank order for comparative (as distinct from absolute) size.

NHM P.6921 – the holotype specimen. The holotype also has a wide array of skeletal elements (1133 parts) from diverse areas of the body (see WOODWARD 1889 for original description, as well as LISTON 2010), including lepidotrichia and gill rakers of particular use for thin-sectioning.

NHM P.11823 – a juvenile/sub-adult specimen. An important specimen for its reduced size of skeletal elements indicating a likely sub-adult or juvenile. This specimen does not include gill rakers, but has some possible lepidotrichial elements as well as some skull elements useful in establishing the rank order matrix referred to above.

The ‘Wallücke’ specimen. This specimen consists of a wide range of unidentifiable meristic and lepidotrichial material, under a range of collection numbers, held mainly by the Westfälisches Museum für Naturkunde in Münster (see LISTON 2010 for a full list of collection numbers and MICHELIS et al. 1996 for a full list of collections). It has been sampled and sectioned a number of times (e.g., WMfN P.20238).

Vaches Noire material. This Callovian material of *Leedsichthys* consists of a series of ceratobranchials and gill rakers in private collections. Sectioned by BARDET et al. (1993), the thin sections were made by the Laboratoire de Paléontologie, Muséum National d’Histoire Naturelle, Paris, France. Only the digital images from the sections were available for study (LISTON 2010).

History of work on histology of *Leedsichthys*

The ‘Wallücke’ specimen

Thin-section analysis of *Leedsichthys* bone was first conducted in 1983 by Martin BÜCHNER, Bielefeld Natural History Museum, to resolve a dispute over whether the fossil fragments, which had been excavated from the Wallücke quarry in the Wiehen Mountains of northern Germany, were animal or plant (LISTON 2010). BÜCHNER observed the presence of both compact (Fig. 5A) and cancellous (Fig. 5B) bone in the fragments. Significant remodelling has taken place, producing a high density of Haversian systems (ENLOW & BROWN 1958). Many of the canals are infilled with sediment (Fig. 5A) and crystalline growth (Fig. 5B). Asymmetrical secondary centripetal deposition of bone (= secondary osteons) can be seen, occasionally blocking former reticular channels (Fig. 5A) and indicating more than one cycle of secondary deposition. Near the poorly ossified or damaged external surface of the bone, there is more evidence of some of the primary bone still remaining between the osteons (Fig. 5A). In contrast, the image of the area of more porous cortical bone shows reticular channels unblocked by further bone growth (Fig. 5B). Although it has not been recorded, which element this section was taken from, the initial bones found were described as ‘reed-like’ in external appearance, leading to their initial misidentification as fossil plant remains (LISTON 2010). Lepidotrichial elements are the only skeletal components of *Leedsichthys* that present this type of appearance. Regardless of its identification, it is clear that the bone underwent a high level of secondary remodelling (THOMASON 1995), and the section does not show any trace of original zones or annuli that may have been present. It is therefore unsuitable for analysis to determine the age of the specimen. This problem has similarly been noted during attempts to count growth rings in other extensively remodelled fossil material (e.g., turtles, SCHEYER & SÁNCHEZ-VILLAGRA 2007).

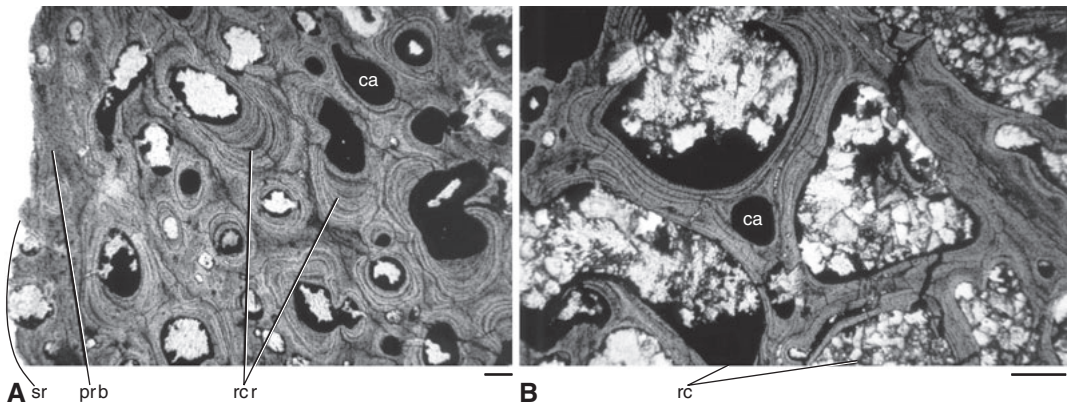


Fig. 5.

Thin-sections cut from lepidotrichia of WMfN PM 17006/8 and photographed by M. BÜCHNER from fragments of the ‘Wallücke’ *Leedsichthys* in 1983, showing compact bone (A) and cancellous bone (B). Abbreviations: **ca**, canal filled with sediment; **prb**, relics of primary bone; **rc**, unblocked reticular channel; **rcr**, reticular channel blocked by remodeling; **sr**, surface of bone showing signs of damage or poor ossification. Scale bars equal approximately 0.1 mm.

Vaches Noire Material

The second time that bones of *Leedsichthys* were sectioned was to resolve a different question of identity. Initially, it was recognized that the fragments represented fossilized vertebrate remains, but the fragments were unfamiliar to those collecting marine reptile remains from the Vaches Noire, Normandie, France. BARDET et al. (1993) sectioned what proved to be part of a *Leedsichthys* ceratobranchial, again finding compact and cancellous bone (Fig. 6A). As LISTON (2007) noted, the sectioned element did not retain any traces of the external fibrous bone that would have contained the hypertrophic and growth zones of cartilage (Fig. 6A) (TAKASHIMA & YOKOTE 1995). Under low-power magnification, a highly dense network of Haversian systems was revealed (Fig. 6B) with far less mineral infilling than in the ‘Wallücke’ section. Even less interstitial primary bone is evident than in the ‘Wallücke’ material, and no annuli or zones are visible, nor any indication whether the primary osteons were laid down in bundles, or radial or circular rows (FRANCILLON-VIEILLOT et al. 1990). The vascular canals are not strictly longitudinal, as they mostly show signs of travelling at angles varying slightly from perpendicular to the plane of sectioning (Fig. 6C), which creates the effect of drift in centripetal deposition within the osteon. In crossed polars, the fibrolamellar constitution of the secondary osteons becomes clear (Fig. 6D). In the section showing the spongy centre (Fig. 6E), the bony framework appears more delicate than in the Wallücke section, with fewer lamellae going to make up supporting ‘struts’ of the trabeculae around the intertrabecular spaces (Fig. 6F). BARDET et al. (1993) reported that the region around the medullary cavity had been subjected to intense remodelling with signs of repeated erosion and reconstruction. They interpreted all of these signs as indicating an animal with a “high metabolic level ... subject to a certain seasonal fluctuation” (BARDET et al. 1993: p. 10). Again, this bone shows signs of annual growth, but the level of bone remodelling prohibits its use in estimation of the age of the specimen. As noted by CASTANET et al. (1993: 261), not all bony elements will record marks of skeletal growth to the same quality (ENLOW & BROWN 1958, BUFFRÉNIL & MAZIN 1990), and in such situations an exploratory survey of the variety of bony elements available is necessary, to assess their relative value for skeletochronological examination.

A further section (GLAHM 109519) was cut from the ‘Wallücke’ specimen of *Leedsichthys* as part of a faunal review by MICHELIS et al. (1996), from what appears to be a cerato/epibranchial junction of the specimen (WMfN P.20238, Fig. 7A,B). MICHELIS et al. (1996) argued that there was no compact bone present on the specimen, and that this absence could be a means for distinguishing between tetrapod bones and *Leedsichthys* in the future (the two have frequently been confused in previous identifications; e.g. HULKE 1887, HUENE 1901). This argument is, however, erroneous for two reasons. First, RICQLES et al. (1991) specifically noted that ‘peculiarities’ of bone histology cannot be regarded as being taxon-specific, and FRANCILLON-VIEILLOT et al. (1990) explicitly stated that the presence or absence of compacta is not

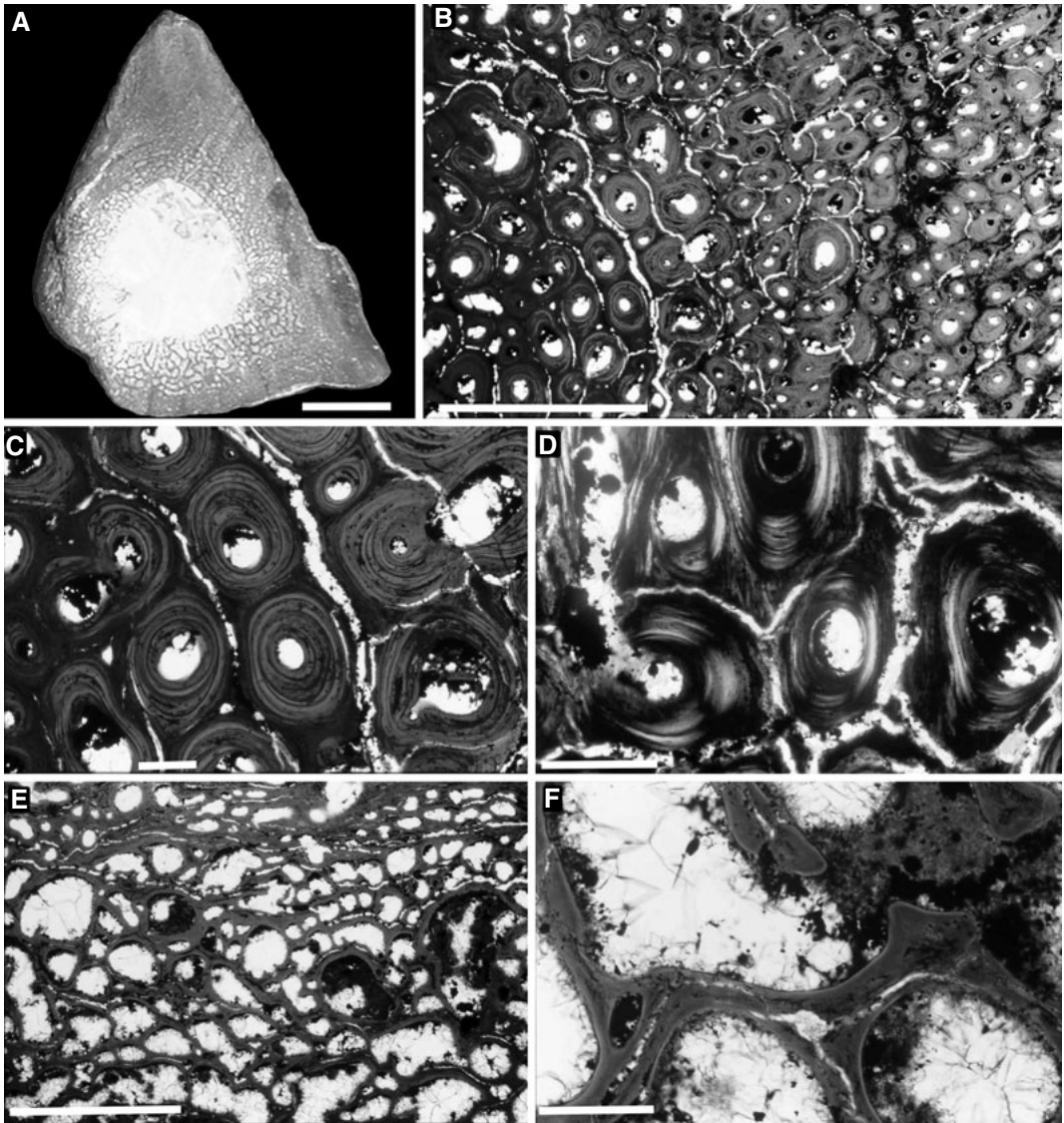


Fig. 6. Branchial specimen of *Leedsichthys* from the Callovian Vaches Noire of Normandie (sectioned by Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France). **A**, ceratobranchial cut to generate thin-section. **B**, general view of compact bone of sectioned ceratobranchial. **C**, detail of Fig. 6B in PPL, showing vascular canals. **D**, detail of Fig. 6B in XPL, showing fibrolamellar bone forming osteons. **E**, general view of cancellous bone, showing spongy centre. **F**, detail of cancellous bone, showing trabeculae with spaces of osteocytes. Scale bars: A-C, E = 1 mm; D, F = 0.1 mm.

diagnostic of precise anatomical or ontogenetic origins. Further, FRANCILLON-VIEILLOT et al. (1990) noted that marine animals can have particular specializations; for example, cetaceans lack true compact bone tissue in their flippers. Second, there is compact bone, approx. 0.2 mm thick, detectable at the top left of this section (Figs. 7B,C), bounding an extensive spongy cortex extending to the medullary cavity. It is, however, unfortunate that MICHELIS et al. (1996) selected a branchial element for sectioning. We know

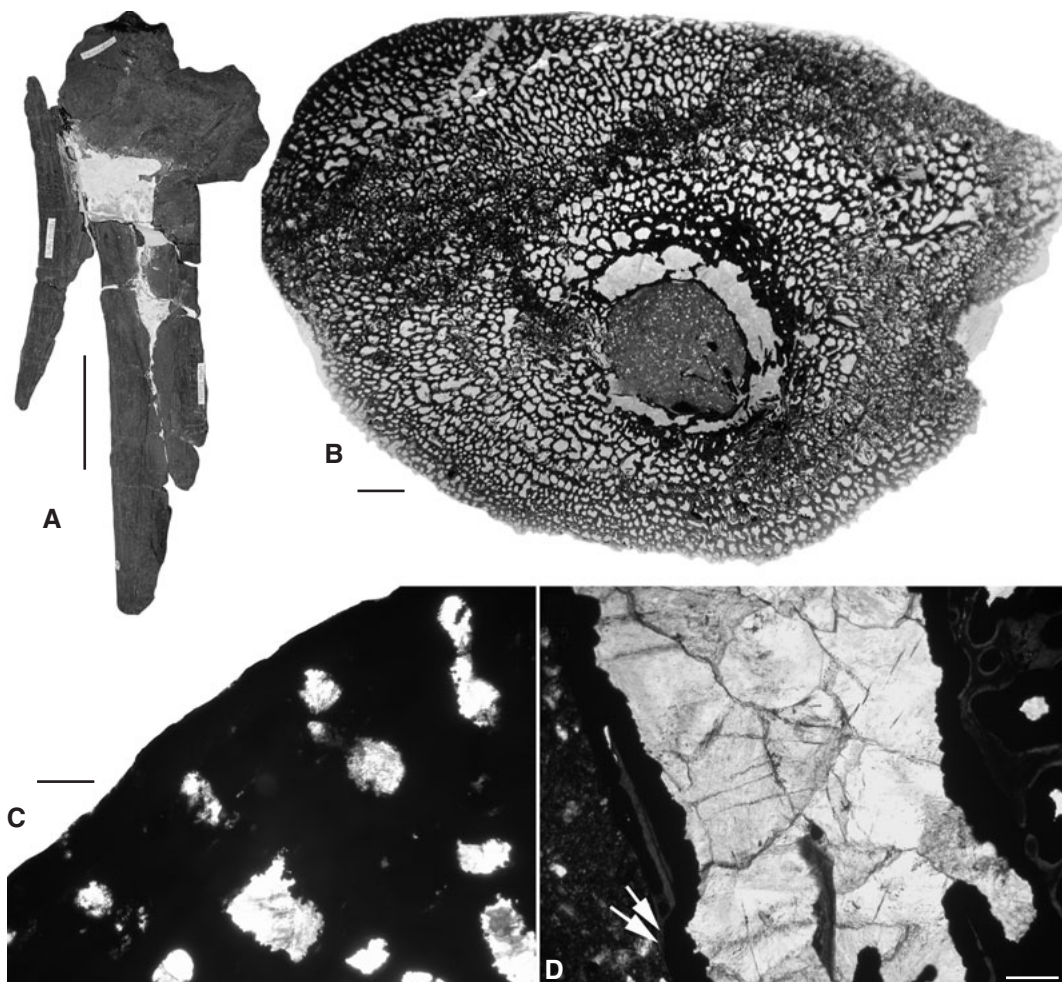


Fig. 7. Branchial specimen (WmfN P20238) of *Leedsichthys* from the Callovian Ornatenton of Wiehengebirge. **A**, specimen is 525 mm long and appears to be an ?epibranchial/ceratobranchial junction. **B**, branchial specimen of *Leedsichthys* from the Callovian Ornatenton of Wiehengebirge; 'Wallücke' thin-section GLAHM 109519 from WmfN P20238. **C**, thin section of branchial specimen (GLAHM 109519) of *Leedsichthys* from the Callovian Ornatenton of Wiehengebirge showing compact bone at surface. **D**, thin section of branchial specimen (GLAHM 109519) of *Leedsichthys* from the Callovian Ornatenton of Wiehengebirge showing intertrabecular space with marks of skeletal growth indicated by arrows. Scale bars: A equals 100 mm; B is approximately 2 mm; C–D are approximately 0.2 mm.

from the histology of living teleosts (e.g., carp) that the ceratobranchial has a thin periosteum bounded internally by a layer of fibrous bone, which in turn covers a thick layer of cartilage (TAKASHIMA & YOKOTE 1995). This means that their selection of this element for sectioning was always unlikely to give them anything more than, at best, an exceptionally thin layer of compact bone.

Close analysis of trabeculae surrounding an intertrabecular space reveals marks of skeletal growth (Fig. 7D), but as part of secondary remodelling they will not be of any value in determining the age of the specimen.

Although structures as fine as reticular channels have been observed, no trace of WILLIAMSON's canals (ENLOW & BROWN 1956) are visible, despite this being a typical feature of holostean bone (RICQLES et al. 1991). Other than this, the characteristics noted in the images of the sections described above

are not surprising. As noted by FRANCILLON-VIEILLOT et al. (1990), in long-lived animals most parts of the cortex consists of dense Haversian systems, with smaller animals having simpler patterns with only moderate Haversian substitution restricted to a bone's cancellous region.

Ideal specimens for sectioning

The sectioned examples from Germany and France reviewed above are unusual, in that most specimens of *Leedsichthys* (including the type material) have not come from these localities, but rather from the brick clay excavated from Peterborough, England. One of the common characteristics of specimens of *Leedsichthys* (from this general locality) is that they are severely crushed (WOODWARD 1889). Crushing is a ubiquitous problem with bones of the dermatocranium of *Leedsichthys*, as they are often found with the compact layers fragmented away from each other. Slender elements appear to retain histological anatomy useful for age quantification; however, large elements lack internal anatomy due to replacement.

During a geochemical study by CHALLANDS & LISTON (2003) it was observed that gill rakers and lepidotrichia clearly record annuli, and that gill rakers record annuli with greater clarity. Gill rakers and/or lepidotrichia occur in about 50 % of the 70 known specimens of *Leedsichthys* (see Annexe in LISTON 2010) suggesting that these relatively common elements are the optimal candidates for age and growth analysis. All other elements are comparatively rare; for example, only one maxilla and one dentary (NHM P.66340, GLAHM V3363) are known out of 50 individuals.

Estimation of age and growth

Criteria for recognizing annuli and measurements

The sections of gill rakers and lepidotrichia present a series of concentric growth marks with broad light zones and narrow darker annular zones in reflected light (Figs. 8–10). These marks are identified as annuli rather than LACs/LAGs (lignes d'arrêt de croissance = lines of arrested growth), as they do not present discontinuities, and are more than double the upper thickness limit of 5 microns for LACs (RICQLES et al. 1991: 38). The sharp lamellar layers also distinguish them from tidal dentinal layers of smaller animals (SOLER-GIJÓN 1999). To accept these lines as tidal markers would result in an excessively accelerated growth rate for such a large fish.

Transects were taken across the polished sections. Transects were selected on the basis of passing through the greatest number of distinct growth marks, avoiding any areas of remodelling wherever possible. For the purposes of measurement in this study, the interface point between the light zones and dark areas was taken as the beginning of a new annulus. The distance from this point on the transect to an arbitrary 'centroid' was measured for each annulus, and the results plotted for each skeletal element. Determination of a central measuring point was problematic, as the external surfaces of the sections are irregular. In all cases, what visually appeared to be the centre of growth within a given section was used.

The annular distances were measured using the Java-based image processing scaling and measuring software ImageJ 1.33u (2004), applied to the photographs taken from the binocular microscope. Where it was not possible to measure all consecutive annuli in a direct line, and a gap was encountered, the last discernible annulus on the line was followed around until a sequence of consecutive annuli could be found to continue the count. Once these annuli could be traced to the next discernible annulus on the original line, the measurements were resumed on the original line. This method provides size data collected in a consistent manner by leaving gaps (i. e., missing data) in the incremental measurement dataset.

Modelling growth profiles

Growth profiles were modelled using regression analysis. Initial examination of the graphed incremental data provided insight into the proper models used for description. Growth curves were then fitted to the data, in order to determine the overall shape of the profiles. Two types of curves were employed for description of the growth profiles: a logistic equation and a BERTALANFFY (1938) growth curve. A logistic growth equation was used in SYSTAT (2007) to describe the growth of gill rakers with S-shaped curves:

$$\text{GRRD}_t = \text{RD}_\infty / 1 + e^{-K(t-t_i)}$$

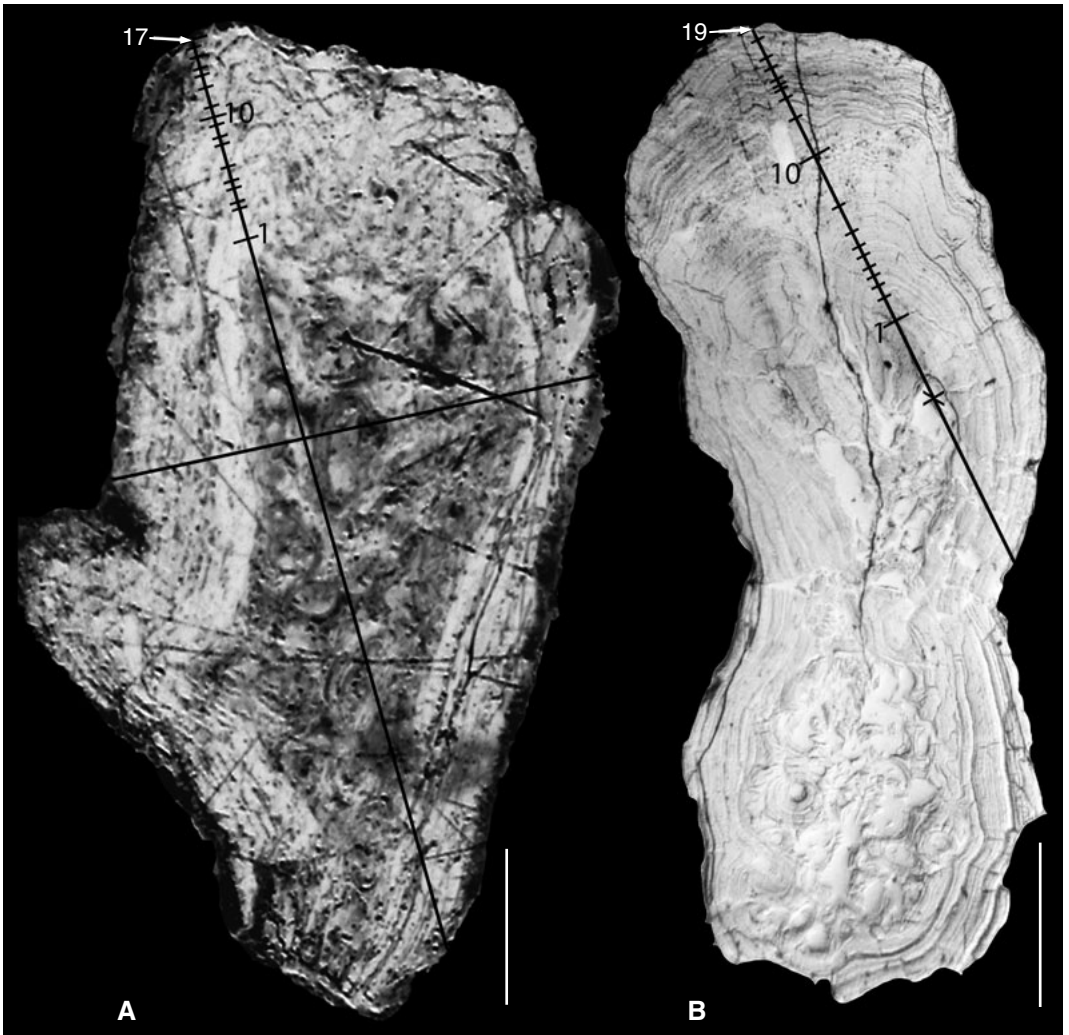


Fig. 8.

Polished sections of gill rakers of *Leedsichthys problematicus*. **A**, gill raker from 'Ariston' (PETMG F174) with 17 annuli and calcified cartilage. **B**, gill raker from 'Tail' specimen (NHM P.10000) with 19 annuli and discontinuities of inner annuli indicating some bone remodelling around a cartilage core. Scale bars = 1 mm.

where the parameters: $GRRD_t$ = gill raker radial distance (mm) at t (age in years); RD_∞ = theoretical maximum RD; K = the BRODY growth coefficient; t = time (i.e., age in years); and t_i = time at inflection point. The inflection point represents a period of accelerated growth creating a sigmoidal shape in the growth profile.

A BERTALANFFY (1938) growth curve (nonlinear regression in SYSTAT 2007) is used to estimate lepidotrichial radial distance:

$$Lpdt RD_t = RD_\infty [1 - e^{-K(t-t_0)}]$$

where the parameters: $Lpdt RD_t$ = lepidotrichial radial distance (mm) at t (age in years); RD_∞ = theoretical maximum RD; K = the BRODY growth coefficient; t = time (i.e., age in years); and t_0 = time at age zero (time at theoretical zero length). Parameters in all tests were examined with 95 % confidence limits.

Estimation of SL

Previous workers have used the growth of a single skeletal element as being proportional to the rate of growth of the entire fish. LEA (1910) used the length of annuli from the centre of herring scales for that purpose (e.g., FROST & KIPLING 1959, PARKER & SCOTT 1965). LEA's work has been taken forward by several workers, with BERTALANFFY (1938) being arguably the most significant innovator followed by PAULY (1994; and see MOREAU 1987 and WOOTTON 1989 for reviews comparing other growth models, such as GOMPERTZ, JOHNSON, logistic, and RICHARDS).

Following on from the work of BURNHAM-CURTIS & BRONTE (1996) and NEWBREY & BOZEK (2003) on scales and otoliths, using LEA's (1910) principle that the annual growth of bony structures is proportional to the annual growth in body length, a BERTALANFFY (1938) growth curve was constructed from the polished sections used above to estimate growth rate in the different examined specimens of *Leedsichthys*.

Results

Estimation of length

To produce estimates of absolute standard lengths, greater emphasis must be placed on specimens other than the 'Gill Basket' specimen, i.e., those with postcranial elements useful for scaling. The Glasgow specimen GLAHM V3363 ('Big Meg') has an extensive series of meristic elements, including ribs, anal fin supports and proximal radial supports for the dorsal fin. Taking the longest element of each type, and comparing it with the Stuttgart Museum's 1.8 m SL *Saurostomus* specimen (SMNS St.56982), produces SL estimates of 11.4 m, 13.3 m, and 14.9 m (taking the base rib width to the centrum as an estimate of vertebra to vertebra length).

This last estimate was discounted, as pleomerism (the tendency for fish species with larger adult size to have more vertebrae than related equivalents, LINDSEY 1988) has often been cited as a mechanism by which bony fishes grow to particularly large size in a given family. The concept of pleomerism is based on the idea that within any one body plan there is an optimal segment number, but that this number changes with body length. WILLISTON's law and DOGIEL's principle of oligomerization both note the general phyletic tendency for number of segments to decrease in fishes in general, and to increase by JORDAN's rule in polar fishes, but to increase in larger forms by pleomerism. LINDSEY (1975) noted this phenomenon in 90 out of 118 fish families studied. In fact, in stating the pleomeristic rule that the number of segments is correlated with characteristic body size among related taxa, LINDSEY (1975) further noted that the relationship is particularly extreme in those fish groups having less complete ossification of the vertebral column, a trait seen in *Leedsichthys*. Although, owing to this lack of ossification, it is not possible to determine whether or not pleomerism occurred in the development of *Leedsichthys*, the preceding comment clearly indicates that it is likely to have been a factor, and so introduces uncertainty that could increase the error for any estimate. Two of the three estimates come from very different postcranial elements and suggest sizes less than 2 m apart; therefore, an average of 12.3 m is used for the SL of this specimen (GLAHM V3363).

For the 'Tail' specimen (NHM P.10000), the lengths of individual caudal lobes (as used by MARTILL 1986a) and the tail span can be used in conjunction with the Stuttgart *Saurostomus* specimen, and estimated lengths of 8.8 and 9.0 m result. Given that the 'Tail' specimen had a significantly shallower ceratohyal depth than 'Big Meg' (GLAHM V3363), it is not surprising that these results are lower than those for 'Big Meg'. Although both these estimates arise from the same skeletal component (and it is therefore unsurprising that they are so similar), an average (8.9 m) will again be used for the estimated length of this specimen.

For 'Ariston' (PETMG F174), comparison of the length of the pectoral fin with the Stuttgart *Saurostomus* specimen results in an estimated SL of 8.0 m. This is consistent with the size ranking established from comparison of hyomandibulae, preopercles, and ceratohyals (see Table 1), and with the comparison between the right pectoral fin of 'Ariston' and the fin fragment of NHM P.10000.

LISTON & NOË (2004) reviewed historical documentation relating to the 'Tail' specimen (NHM P.10000), including an account written by LEEDS (in a letter to A. S. WOODWARD) of the unexcavated specimen, reported as though at least some of the postcranial parts of the animal had been found approximating a life position. LEEDS refers to two fins lying just behind the head and that "back some 12 or 18 feet was found the tail". This has particular relevance to the current study. Although LEEDS did not give an interpretation of the two fins, a part of one of them was purchased as a pectoral, and he declares

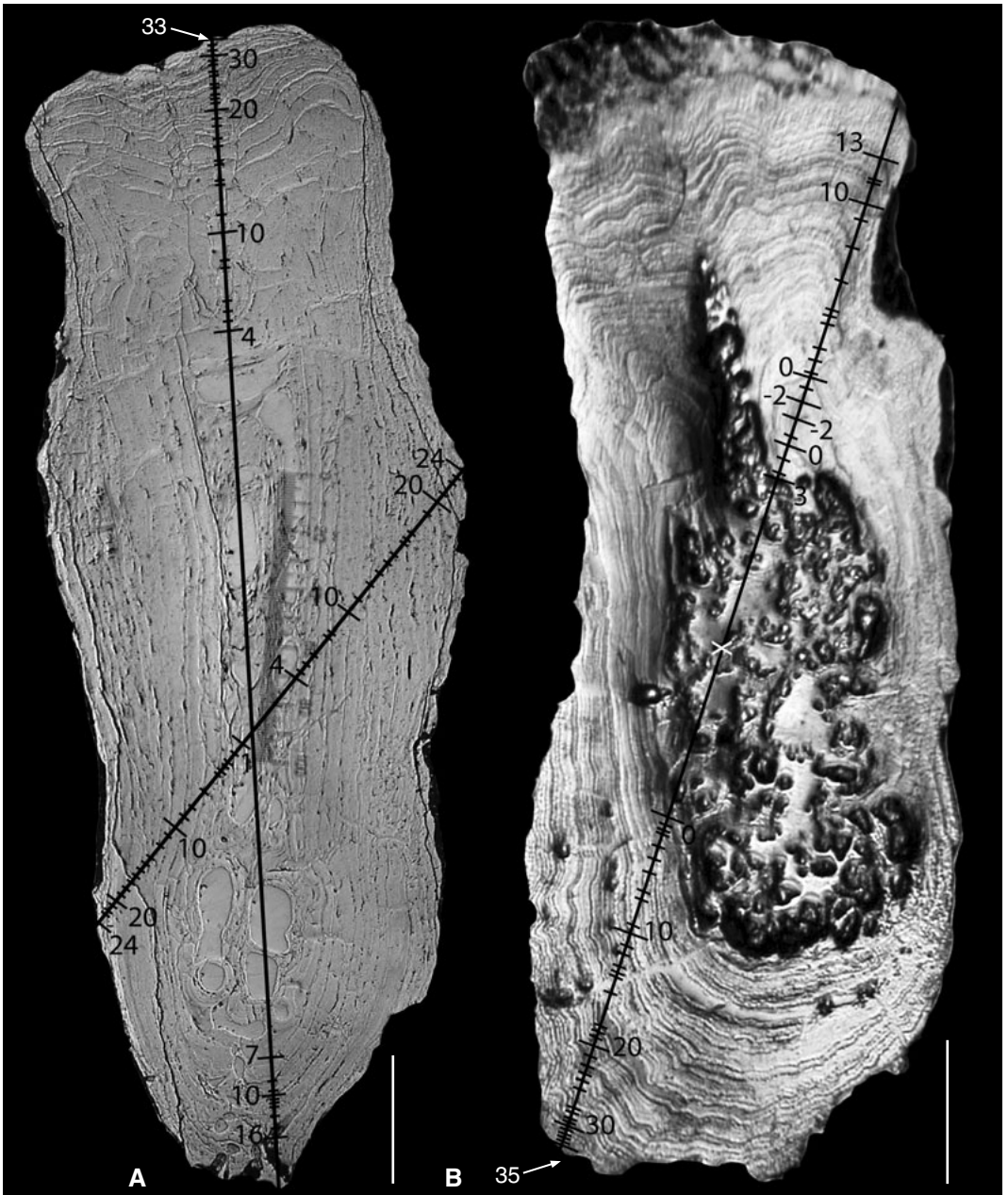
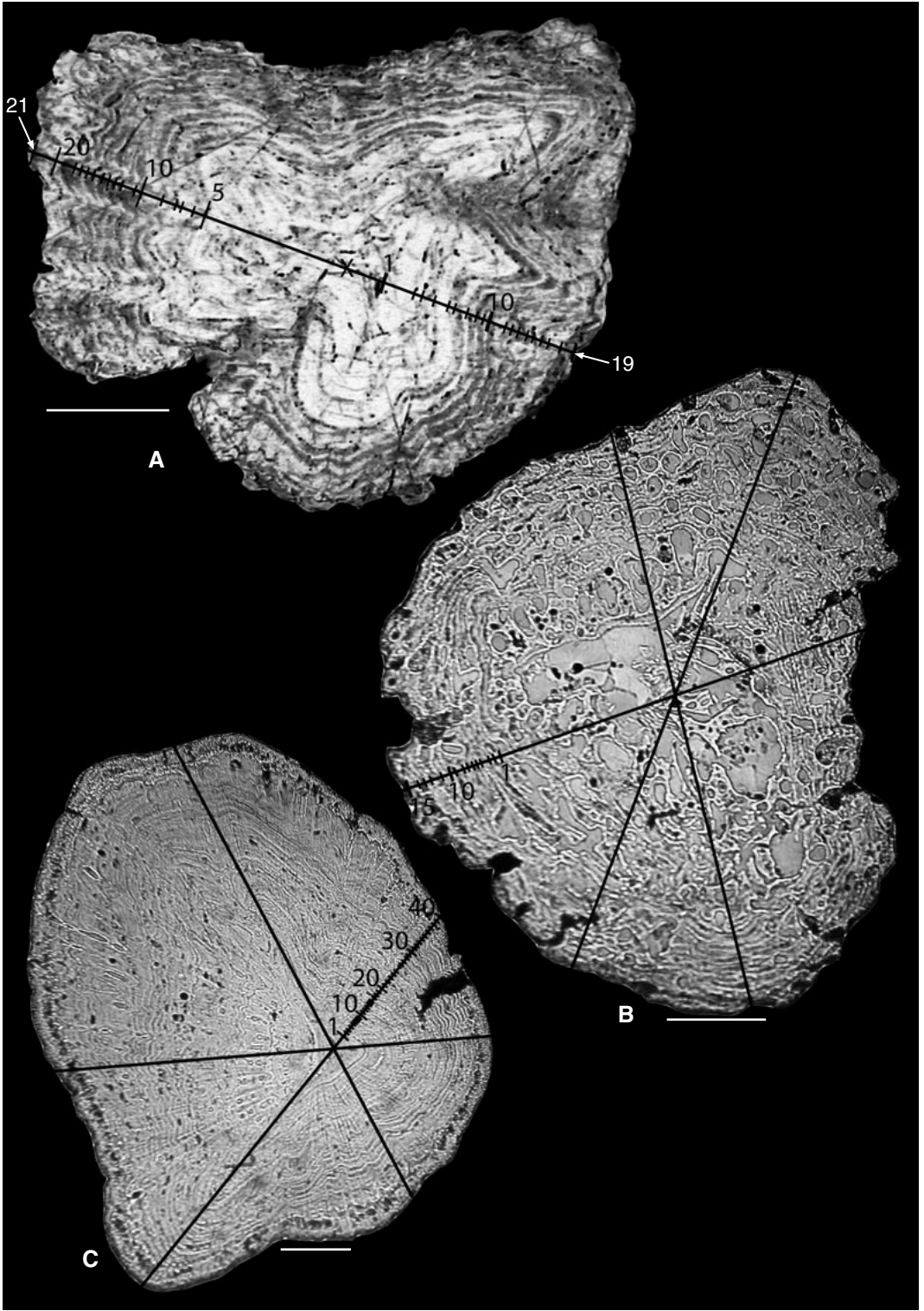


Fig. 9. Polished sections of gill rakers of *Leedsichthys problematicus*. **A**, gill raker from holotype specimen (NHM P.6921) with 33 annuli and inner bone remodeling. **B**, gill raker from 'Gill Basket' specimen (NHM P.10156) with 38 annuli and pyrite infill of a resorbed core. Scale bars = 1 mm.

Fig. 10. Polished sections of bones from *Leedsichthys problematicus*. **A**, lepidotrichial fragment from 'Ariston' (PETMG F174) with 21 annuli. **B**, fragment of an unidentifiable meristic element from 'Big Meg' (GLAHM V3363) showing 15 annuli and inner bone remodeling. **C**, lepidotrichial fragment from holotype specimen (NHM P.6921) with 40 annuli. Scale bars = 1 mm.



in the letter that he did not believe that he had found the dorsal fin of the specimen. Pelvic fins are rare in large pachycormids; the 1 m long *Orthocormus* is the only exception (LAMBERS 1988). If the pelvic fin is omitted from consideration (no bones related to the pelvic fin have ever been reported or collected for *Leedsichthys*), this leaves two possible interpretations of his words: 1) the two fins are both pectorals (he stated only that they are 'a good distance apart' without specifying if the separation is related to the width of the animal or its length); or 2) one is a pectoral fin and the other is the anal fin. LEEDS' letter indicates a distance between the 'last' of these fins and the tail as "12 or 18 feet" (3.5 or 5.5 m). It seems reasonable to use an average figure for this distance of 4.5 m. In large pachycormids, the post-pectoral distance ranges from 73 % (from the largest specimens) to 80 % of the SL, and the post-anal fin length ranges from 32 % (from the largest) to 42 % of the SL. If the distance quoted in the letter refers to the distance between the pectoral fins and the caudal fin, this suggests a range of roughly 5.6–6.2 m. If the distance referred to is the distance between the anal fin and the caudal fin, then the range of sizes suggested is 10.7–14.1 m. The two indices for estimating SL of the 'Tail' specimen suggest a minimum to maximum range of 5.6–14.0 m, which encompasses the size of the first estimate of 8.9 m.

Counts of annuli and shapes of growth profiles

As the number of growth marks appears to increase from section to section, so the degree of internal remodelling and resorption appears to increase within the gill rakers. A high level of vascularisation also poses a problem (in terms of visibility of annuli) within unidentifiable meristic elements of two specimens sampled from 'Big Meg' and 'Ariston'. However, resorption did not appear to present a significant problem with sampled lepidotrichia.

Full listings of measurements of annuli are given in Table 2.

'Ariston' specimen (PETMG F174). Three elements were sampled from this specimen; the lepidotrichium presents 21 annuli, compared to 17 in the gill raker (Table 2). Both plots display a linear pattern after an initial steep period of growth (Fig. 11). The gill raker shows signs of a calcified cartilage centre, with partial erosion of the innermost remaining annuli (Fig. 8A), whereas the lepidotrichium does not (Fig. 10A). When sectioned, the unidentifiable meristic element (PETMG F174/element 264) was found to be extensively remodelled, and unsuitable for use.

'Tail' specimen (NHM P.10000). The gill raker sectioned reveals 19 annuli, again with signs of resorption at the edge of the innermost annuli around a cartilage core, but to the least degree of any gill raker sampled (Fig. 8B, Table 2). The growth profile shows a clear sigmoidal pattern, with an inflection at 10 annuli representing the smallest sizes of any of the sampled specimens (Fig. 11A). The small size of the youngest ages suggests little to no remodelling compared to the other specimens.

'Big Meg' specimen (GLAHM V3363). An unidentifiable meristic element shows only 15 annuli (Table 2), but about 60 % of the core of the element is resorbed (Fig. 10B). On this basis, comparing it with the other meristic lepidotrichial elements sampled from the other specimens, it was estimated that around 12–16 annuli had been resorbed.

Holotype (NHM P.6921). The gill raker shows 36 annuli, 33 in a single transect (Fig. 9A, Table 2) with signs of internal resorption of annuli, as with other sectioned gill raker specimens (Figs. 8, 9). The lepidotrichial fragment shows 40 annuli (Fig. 10C). The gill raker again displays a sigmoidal pattern of growth (Fig. 11A), and the lepidotrichium is characterized by an initial period of fast growth followed by a tapered, relatively linear growth profile (Fig. 11B).

'Gill Basket' specimen (NHM P.10156). The gill raker shows 38 annuli in a single transect with 2 earlier annuli also visible, significant internal resorption and remodelling (Fig. 9B, Table 2). This gill raker has a sigmoidal growth profile, albeit less pronounced over a much larger number of annuli than that for any other gill raker (Fig. 11A).

Comparison of resorption, age, and growth among elements

As can be seen in Figure 11B, both of the sampled lepidotrichia (PETMG F174, NHM P.6921) display signs of rapid growth (between 25 % and 40 %) early in life. The corresponding gill rakers (Fig. 11A) show a slower growth with shallow profiles. Gill raker specimens also show consistently fewer annuli than do lepidotrichia because of internal remodelling and resorption of earlier annuli.

Because the ‘Tail’ specimen has the most data for growth at young ages, it was modelled with the logistic growth equation to demonstrate the inflection in the growth profile (Fig. 11A). The inflection point represents a period of accelerated growth, creating a sigmoidal shape in the growth profile, with the logistic regression crossing at the point of inflection ($r^2=0.982$, $GRRD_{\infty}=2.925$ [95 % C.I.=2.831–3.018], GR BRODY growth coefficient [K]=0.201 [95 % C.I.=0.180–0.221], set $t_i=9$). Assuming a common inflection point of growth among gill rakers of all individuals, it was possible to adjust the ages of other profiles

Table 2.

Measurements of annuli and unadjusted ages of *Leedsichthys problematicus* (all in mm) with adjusted ages from inflection calibration associated with gill rakers. Corrections are noted by “-”. Abbreviations: GR, gill raker; LPDT, lepidotrichium; ME, meristic element.

Annulus Number	PETMG	PETMG		BMNH	GLAHM	BMNH		BMNH	BMNH	BMNH	
	F174 LPDT	F174 GR	GR	P.10000 GR	V3363 ME	P.6921 GR		P.6921 (SW) LPDT	P.6921 (NE) LPDT	P.10156 GR	
		adjusted				adjusted				adjusted	
1	0.33	1.37	-	0.51	1.88	-	-	0.98	0.26	-	-
2	0.59	1.57	-	0.68	1.95	-	-	-	0.44	-	-
3	0.94	1.62	-	0.74	2.00	-	-	1.80	0.50	1.23	1.23
4	1.09	1.71	-	0.81	2.05	2.71	-	1.90	0.53	1.32	1.32
5	1.24	1.78	-	0.87	2.11	2.78	2.71	1.98	0.56	1.39	1.39
6	1.28	1.84	-	0.98	2.15	2.86	2.78	2.04	0.60	1.43	1.43
7	1.35	1.98	-	1.06	2.22	2.95	2.86	-	0.62	1.46	1.46
8	1.50	2.07	-	1.22	2.27	3.21	2.95	2.24	-	1.56	1.56
9	1.65	2.16	-	1.34	2.34	3.29	3.21	2.40	0.69	1.63	1.63
10	1.72	2.24	1.37	1.63	2.41	3.62	3.29	2.49	0.72	1.78	1.78
11	1.82	2.29	1.57	1.90	2.45	3.72	3.62	2.62	0.77	1.88	1.88
12	1.89	2.41	1.62	2.03	2.56	3.84	3.72	2.72	0.81	2.02	2.02
13	2.01	2.49	1.71	2.12	2.63	3.89	3.84	-	0.85	2.09	2.09
14	2.06	2.53	1.78	2.15	2.68	3.98	3.89	-	0.90	2.18	2.18
15	2.10	2.59	1.84	2.23	2.73	4.04	3.98	2.87	0.92	2.24	2.24
16	2.18	2.67	1.98	2.31	-	4.14	4.04	-	0.96	2.32	2.32
17	2.26	2.72	2.07	2.33	-	4.20	4.14	3.01	1.05	2.38	2.38
18	2.37	-	2.16	2.45	-	4.24	4.20	-	1.14	2.42	2.42
19	2.44	-	2.24	2.52	-	4.29	4.24	-	1.18	2.60	2.60
20	2.65	-	2.29	-	-	4.36	4.29	3.14	1.25	2.66	2.66
21	2.77	-	2.41	-	-	4.41	4.36	3.19	1.28	2.71	2.71
22	-	-	2.49	-	-	4.45	4.41	3.24	1.31	2.75	2.75
23	-	-	2.53	-	-	4.48	4.45	3.30	1.35	2.77	2.77
24	-	-	2.59	-	-	4.51	4.48	3.35	1.39	2.80	2.80
25	-	-	2.67	-	-	4.54	4.51	-	1.43	2.87	2.87
26	-	-	2.72	-	-	4.59	4.54	-	1.54	2.91	2.91
27	-	-	-	-	-	4.63	4.59	-	1.62	3.02	3.02
28	-	-	-	-	-	4.69	4.63	-	1.68	3.07	3.07
29	-	-	-	-	-	4.73	4.69	-	1.76	3.11	3.11
30	-	-	-	-	-	4.78	4.73	-	1.82	3.16	3.16
31	-	-	-	-	-	4.83	4.78	-	1.89	3.26	3.26
32	-	-	-	-	-	4.89	4.83	-	1.93	3.30	3.30
33	-	-	-	-	-	4.95	4.89	-	1.96	3.36	3.36
34	-	-	-	-	-	-	4.95	3.53	1.99	3.37	3.37
35	-	-	-	-	-	-	-	3.61	2.04	3.41	3.41
36	-	-	-	-	-	-	-	3.70	2.09	3.46	3.46
37	-	-	-	-	-	-	-	3.83	2.16	3.51	3.51
38	-	-	-	-	-	-	-	3.90	2.21	3.55	3.55
39	-	-	-	-	-	-	-	3.99	2.27	-	-
40	-	-	-	-	-	-	-	4.03	2.32	-	-

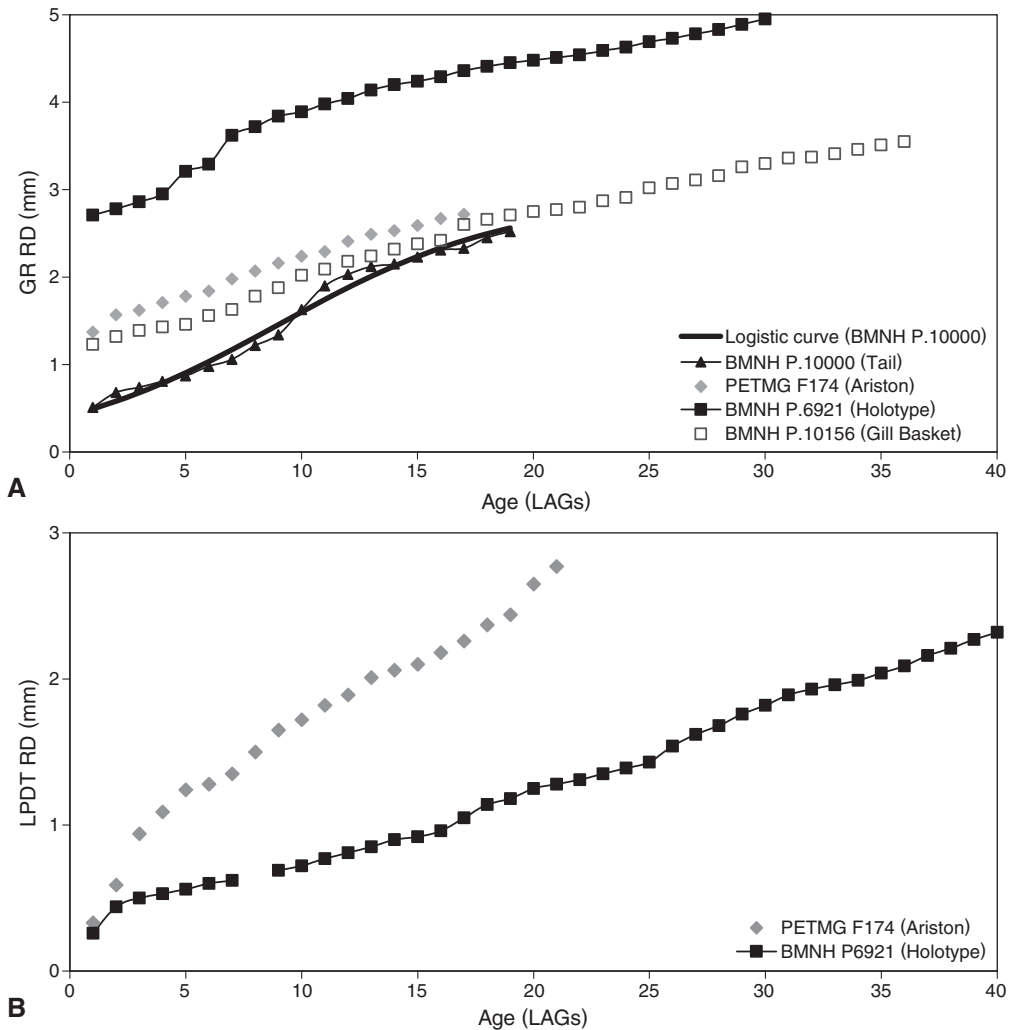


Fig. 11. Growth profiles of *Leedsichthys problematicus*; each symbol represents a growth series from a single specimen. **A**, growth profiles from four gill rakers (GR) as measured in radial distance (RD) with regard to the number of annuli; solid black line represents a significant logistic regression describing the shape of the NHM P.10000 growth profile as sigmoidal. **B**, growth profiles from lepidotrichia (LPDT).

by aligning their inflection points with that of the ‘Tail’ specimen. This suggests as many as 2–10 annuli are missing due to resorption near the centres of the other specimens (Table 2, Fig. 12A). For example, aligning the inflection points of the ‘Gill Basket’ specimen with the ‘Tail’ specimen suggests that two annuli are resorbed. This correlation gives a figure of a minimum age in years for each individual based solely on the lowest possible number of annuli lost due to resorption or non-ossification in the gill raker. Visual estimates of numbers of gill raker annuli lost through resorption or non-ossification were also made through comparison of sections.

In contrast to the results for gill rakers, no such sigmoidal pattern is visible for the lepidotrichia, which have more of a convex growth curve and are better modelled by a BERTALANFFY (1938) growth equation (Fig. 12B). This technique produced a slightly convex BERTALANFFY growth curve for the holotype (NHM P.6921) with two significant parameters (Fig. 12B, $r^2=0.978$); it predicts a RD_{∞} of 5 mm (95 % confidence

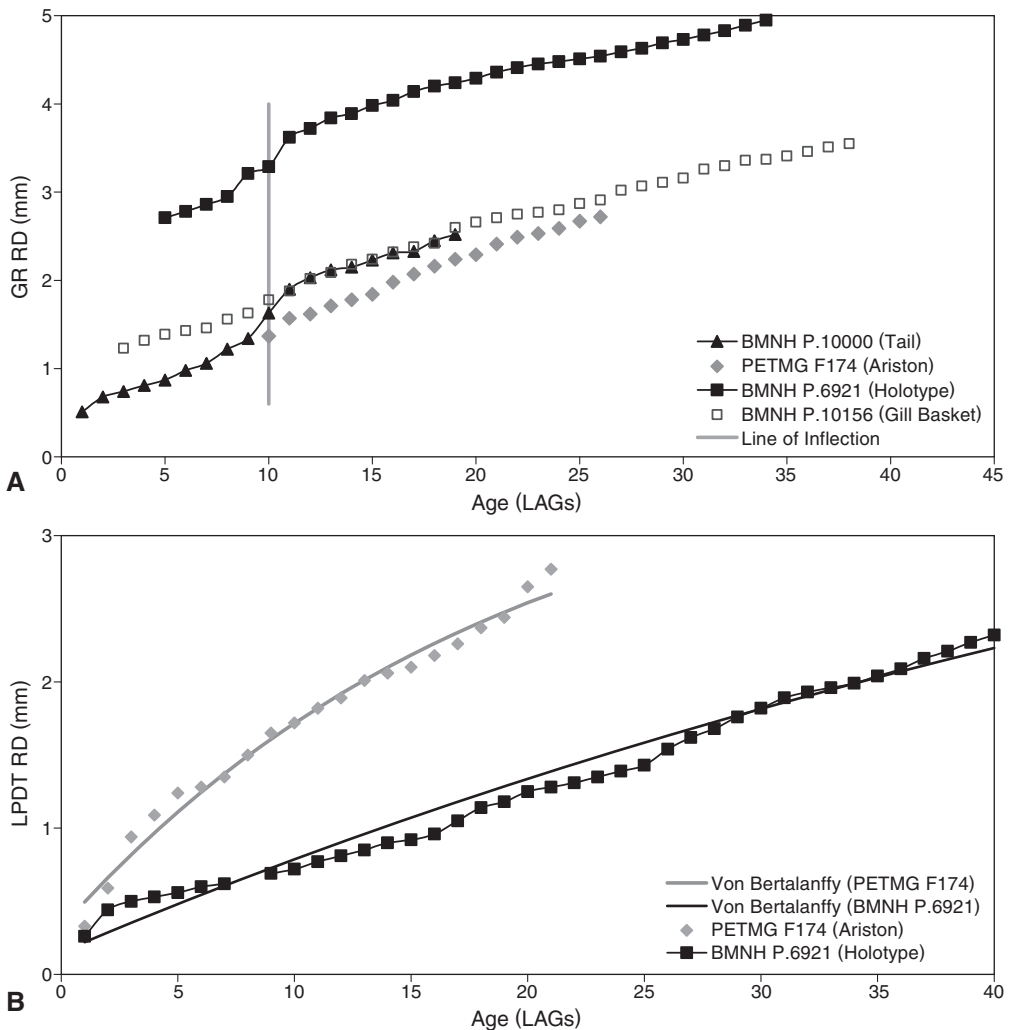


Fig. 12.

Growth profiles of *Leedsichthys problematicus*; each symbol represents a growth series from a single specimen. **A**, growth profiles from four gill rakers (GR) as measured in radial distance (RD) with regard to the number of annuli; solid grey line represents an inflection in the sigmoidal curve of NHM P.10000 and is used to calibrate the ages of the other sigmoidal growth profiles by lining up their inflections. **B**, growth profiles derived from lepidotrichia (LPDT).

interval [C.I.] = 2.383–7.617 mm), a BRODY growth coefficient (K) of 0.014 (95 % C.I. = 0.004–0.023 K), and an age of –2.6 years for a radial diameter of zero mm (95 % C.I. = –4.063 – –0.389 years). The second growth profile is also a high, convex BERTALANFFY growth curve ('Ariston', PETMG F174) with three significant parameters (Fig. 12B, $r^2 = 0.978$); it predicts a RD_{∞} of 3.718 mm (95 % C.I. = 2.795–4.641 mm), a BRODY growth coefficient (K) of 0.053 (95 % C.I. = 0.028–0.078 K), and an age of –1.691 years for a radial diameter of zero mm (95 % C.I. = –2.899 – –0.484 years).

The sample taken from GLAHM V3363 (Fig. 10B) indicates a highly vascularised bone with roughly 60 % of its core having been resorbed, and only 15 annuli detectable at its periphery. Internal remodelling is even more noticeable in NHM P.10156, where post-depositional pyrite had developed secondarily, replacing much of the secondary bone, and occasionally appearing down primary vascular canals (Fig. 9B).

Some 38 annuli are still clearly visible in this specimen, indicating that the actual number of annuli laid down during life is likely to be much higher. Although these last two specimens lack a definitive annular count that could give a constrained age estimate, the levels of internal resorption suggest greater age than other specimens, and are consistent with the initial large estimates of their SL within the sample group.

Table 3 summarizes estimates of annuli, ‘missing’ annuli, the estimated sizes from scaling and the estimated ages after visual comparison for resorption or non-ossification.

Discussion

Estimation of size by scaling of skeletal elements

As noted by LISTON & NOË (2004), the selection of skeletal elements for scaling is not a simple task, as radically different estimates of SL can result from among the remains of an individual. This is particularly evident when skull elements, especially components of the gill basket in fishes, are used. One particular explanation for such a striking difference in estimates is that the gill basket of a fish bears the respiratory surface of the gill filaments. This is effectively a two dimensional surface, whose square will vary with the cube of the mass of the body (or the volume of the blood to be oxygenated) that it has to supply with oxygen (MATTHEWS & PARKER 1950). With increasing size, this leads to an animal with a disproportionately large gill basket for the length of its body, because a higher number of lamellae are required to meet the increased oxygen needs of the larger animal (HUGHES 1984), and because extending the length of the gill filaments themselves does not make a significant difference to oxygen absorption from the water beyond the first 2–2.5 mm (FREEDMAN & NOAKES 2002). As PAULY (1984: p. 282) puts it: “gills cannot grow as fast as the body they have to supply ... because a surface, even when growing with a strong positive allometry, cannot keep up with a growing volume ...”.

Pachycormids and unossified skeletal elements

The phyletic trend across the family Pachycormidae is towards reduced skeletal ossification with taxa of increasing adult size (LISTON 2007, 2008a; FRIEDMAN et al. 2010). This is particularly evident in the meristic vertebral elements, as vertebral components are reduced from being fully present in small adults of *Haasichthys* (274 mm SL, DELSATE 1999: fig. 2), to only vertebral arches being present in *Hypocormus* (750 mm SL, GOODRICH 1930: fig. 46), two sections of the vertebral column only being partially present in *Pachycormus macropterus* (64 cm TL, HAUFF & HAUFF 1981: fig. 94), only posteriorly present in other members of the family, and finally absent in *Saurostomus* (1.3 m TL, HAUFF & HAUFF 1981: fig. 93) and *Martillichthys* (2.1 m SL, LISTON 2008a: fig. 1). The possibility of further reduction, including the absence of ossified pleural ribs, is hinted at by other large specimens (e.g., *Ohmdenia multidentata*, 2.3 m TL, HAUFF 1953: plate 4) and an unidentified specimen of *Pachycormus* of about 85 cm length, which may yet prove to be an undescribed species (HAUFF & HAUFF 1981: fig. 96). The loss of some dermal skull elements in *Saurostomus esocinus* has also been documented (WOODWARD 1916: pl. II). *Leedsichthys problematicus* exhibits the preservation of discrete areas of its body, suggesting a further loss of ossified elements. The Cretaceous pachycormid *Protosphyraena* is preserved in a similar manner, where only select clumps of its body are found, despite its apparently prodigious size, as evidenced by its tail span of 685 mm (MCCLUNG 1908).

The non-ossification of skeletal elements is not as problematic for fishes as for terrestrial animals. Support of body weight is not generally a primary function of the skeleton in fishes (BERRIOS-LOPEZ

Table 3. Comparison of size and age estimations for five specimens of *Leedsichthys*.

	Ariston PETMG F174	Tail NHMUK PV P10000	Big Meg GLAHM V3363	Holotype NHMUK PV P6921	Gill Basket NHMUK PV P10156
Estimated length	8.0 m	8.9 m	12.3 m		16.5 m
Maximum ring no. gill raker	17	19		33	38
Maximum ring no. LpdT	21		15	40	
Line of inflection modifier	+9	0		+4	+2
Estimated age (yrs)	26	19		40	38

et al. 1996): reduced mass in fishes is more likely to reflect the need to lower moments of inertia, thus minimising the energy required for acceleration and deceleration in water (BIEWENER 1983), as witnessed in dolphins (BUFFRÉNIL & MAZIN 1990). WEBB & BUFFRÉNIL (1990) have suggested that there would be less need for this reduction in overall skeletal mass in larger aquatic vertebrates, as their need for higher manoeuvrability is constrained by their prey choices (“culminating in filter feeding”, WEBB & BUFFRÉNIL 1990). This hypothesis ignores the physical limitations on non-teleostean actinopterygians (WOODWARD 1916, ARRATIA 1999) such as pachycormids, where the lack of a gas-bladder (an organ often cited as a specifically teleost character, FREEDMAN & NOAKES 2002) would necessitate significant work against gravity for extremely large fishes that had to feed near the surface. Therefore, any means of reducing buoyancy problems associated with the development of large size, including the reduction of overall skeletal mass by having a higher proportion of the skeleton as cartilage, is likely to have been favoured.

Potential for preservation of bones with annuli

The selection of skeletal elements is further complicated for this taxon by the extremely reduced ossification of the skeleton, compromising the preservation potential for much of its remains. This is demonstrated by specimens such as the ‘Tail’, where the caudal rays are extremely well preserved on a very fine scale, with the lobes discovered lying in life orientation relative to each other (LISTON & NOË 2004), indicating minimal transportation and disruption to the specimen after death. Yet none of the presumably larger supporting elements at the core (e.g. hypural plate, epurals) are present. Although post-mortem scavenging activity on the carcass is indicated by the presence of a hyodont tooth in the pectoral fin fragment of this individual (Fig. 2B), it is unlikely that these elements were separated from the carcass post mortem, as most of the delicate structures of the proximal extremities of the caudal fin have remained intact. Instead, it seems more likely that the elements simply were not ossified and thus were not preserved. Support for this is provided by the absence of any similar supporting elements from all other remains of *Leedsichthys* (LISTON 2010).

The lack of ossification of elements of the skeleton has been a problem for workers on *Leedsichthys* since it was first fully described (WOODWARD 1889). JØRGENSEN (1966) noted reductions in the skeletal mass of pelagic suspension feeders and interpreted this as a reflection of the very limited food supply reaching that depth (1000–4000 m) of the water column. TAYLOR et al. (1983) made similar observations with regard to reduced skeletal development of various mesopelagic teleosts and the extremely poor calcification (relative to other lamniform sharks) of the skeleton of *Megachasma pelagios* in its deep-water oceanic habitat. In contrast, the Oxford Clay epeiric sea was suggested to have been 50–200 m in depth (MARTILL et al. 1994), with high productivity (HUDSON & MARTILL 1991). Thus, reduced skeletal development seems to be a strategy that is not dictated by limitations of nutrient supply, even though it has restricted the number of elements that are preserved with annuli.

Amongst preserved elements, many are remineralised, eradicating annuli that may have been present. Resorption of bone is a natural part of bone growth for many organisms (first noted by John HUNTER in 1772, and published posthumously by his assistant Everard HOME in 1798). Although the gill rakers contain clear and distinct annuli, they are variably affected by resorption. The measured dimensions of raker sections ranged widely, reflecting the variable size of the rakers within an individual. Although the lepidotrichial fragments shed more light on the early period of growth, they do not appear to provide enough information to illustrate in detail the first 1–2 years of growth.

It has previously been demonstrated that there are problems with the first year of growth not being recorded in scales of osteichthyans (CASSELMAN 1996). As noted earlier, ossification is selective and skeletal ossification is negatively correlated with increasing adult SL in the family Pachycormidae. Heterochronic ossification has been reported in both cranial (BLOCK & MABEE 2012) and post-cranial (TONG et al. 2012) components of the skeleton of osteichthyans, and it is possible that the partial ossification of pachycormid skeletons is a result of paedomorphosis within such a heterochronic system. Delayed initial ossification would be another means of potentially ‘losing’ annuli from the total count within a preserved skeletal component.

Gill rakers and lepidotrichia as analogs for growth of the whole animal

Despite the similarity of the size estimates to growth curves derived from lepidotrichia (3.5–4.8 % difference range), it could be that neither the gill raker nor the lepidotrichium is a good analogue for the growth of the whole animal. As CASTANET et al. (1993) noted, a single section from one bone may not be representative of the skeleton as a whole. BURNHAM-CURTIS & BRONTE (1996) made a distinction between otoliths and scales for lake trout, determining that the sagittae provided a more accurate model for the growth of the whole animal. LEA (1910) referred to variability of results from measurements on different scales depending on the suitability of a given scale for estimation of body length. Given differences in rates of growth produced simply by varying the angle of transects through a raker or lepidotrichium, it is clear that absolute estimates of rate of growth must be approached with caution when employing this method. On the other hand, the raker or lepidotrichial elements might be effective analogs for the growth profiles of *Leedsichthys problematicus*, yet lack sufficient resolution to show the youngest annuli.

Interpretation of the growth profiles

Growth profiles may be linear, curvilinear or sigmoidal (DAS 1994). The gill raker profiles gave a consistently sigmoidal pattern, which could be used to align and overlay the growth profiles of different specimens. When this was done, an inflection at the minimum age of 10 annuli appeared to be key. Such inflections in growth are often related to the onset of sexual maturity in an animal, with an increase in girth and/or body mass, although sexual maturity might be unlikely, as it does not appear that *Leedsichthys* had reached two thirds of its 'final body length' by this stage in its growth (CASE 1978). Alternatively, as noted earlier, the increasing respiratory load of a growing fish means an increase in the numbers of gill lamellae proportionate to the volume of the fish's body (PAULY 1984). The primary function of gill rakers in osteichthyans is a defensive one, to protect the delicate gill lamellae (LOY et al. 1999). Increase in size of lamellae could be correlated with a need for increased gill raker cover possibly including enlargement of gill rakers. A secondary function in suspension feeders such as *Leedsichthys* is that gill rakers have an important role in feeding. Some osteichthyans go through non-suspension feeding stages before growing to their suspension feeding length (LOY et al. 1999). Therefore, the inflection (Fig. 12A) might well represent that time in the growth of these fishes.

The growth profiles recorded in the lepidotrichia reflect the total curvilinear growth of the animal. The lack of an "asymptote" (or even the indication of the approach of one) in the growth of any of the lepidotrichia, combined with the pattern of consistent but extremely slow growth for all but the first two years of annuli recorded in the sections, makes a sigmoidal pattern of growth for these elements very unlikely. Slow growth is characteristic of longer-lived fishes (CARLANDER 1969, BURNHAM-CURTIS & BRONTE 1996, NEWBREY et al. 2008). Rather than reflecting an entirely linear lifetime growth pattern, growth may have been fast for the first 1–2 years of life. Rapid postnatal growth has also been noted for contemporary marine vertebrates (such as lamnids, scombroids, and cetaceans) that have a thunniform morphology (BUFFRÉNIL & MAZIN 1990).

Fast early growth gives protection from predators, but as NIKOLSKY (1963) notes, it is only possible in the presence of an abundant food supply, and its attendant risk of increased exposure to predators (HELFMAN et al. 1997). HUDSON & MARTILL (1991) and MacQUAKER (1994) have both written on the high levels of primary production in the Oxford Clay sea. The mean organic carbon content for the Lower Oxford Clay (= Peterborough Member, COX et al. 1992) is 5.1 %, and there is a large amount of accumulated organic matter mainly from marine phytoplankton. CASSELMAN (1996: 83) noted that the availability of prey "directly affects the size relations between calcified structures and the body".

Evaluation of growth parameters

There is agreement between the rank order of sizes of individual bones and the estimated sizes of the total animals, arrived at independently of those individual bones. Although individual body size is not always a sound indicator of relative age (CASTANET et al. 1993: 269), there is some agreement between the rank order of sizes and that of ages of the specimens derived from annuli (Liston 2007). All of these lines of evidence support the initial hypothesis that the 'Ariston' specimen is a younger individual than the 'Tail' specimen, and indeed younger than any of the other specimens in the sample group with the exception of GLAHM P.11823 (Table 1).

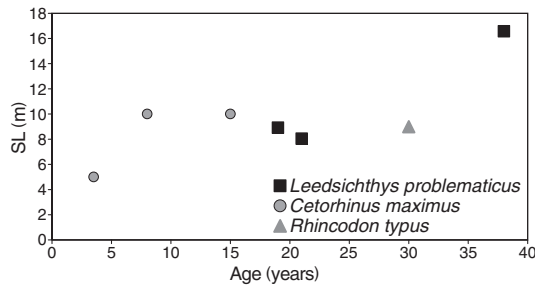


Fig. 13.

Comparison of SL at age of *Leedsichthys problematicus* and two large filter feeding chondrichthyans; the basking shark, *Cetorhinus maximus* and the whale shark, *Rhincodon typus*.

The natural modern analogs for *Leedsichthys* are the whale shark, *Rhincodon typus*, and the basking shark, *Cetorhinus maximus*, as both are large, pelagic suspension feeders. There is scant information on the size and growth of the whale shark: most sighted individuals are between 3 and 10 m in length (UCHIDA 1983, CLARK & NELSON 1997), with the longest individual reliably reported as 12 m (COLMAN 1997), although other sources anecdotally report higher figures (COMPAGNO 2001). The only estimates for size-at-age relate to the minimum for maturity, being a SL of over 9 m and an age of over 30 years (COLMAN 1997).

SIMS et al. (2003) noted that the habitat of the basking shark was primarily in water depths less than 200 m, which is reminiscent of interpretations of the depth of the Oxford Clay sea (MARTILL et al. 1994). Although there is slightly more length-at-age data in the literature for the basking shark than for the whale shark, there are potential problems with the data. Recent work by NATANSON et al. (2008) explored the problems originally highlighted by PARKER & STOTT (1965) with the use of putative ‘annuli’ from basking shark centra. The vertebral bands present seem to be more related to girth than age and thus vary according to position in the body. The differences along the vertebral column are minimal for small or large underweight sharks, but increase with total length. However, the length-at-age estimates in the work of SIMS et al. (1997) appear to be more based on year-on-year observations of individuals and use of BERTALANFFY growth curves, and therefore are useful for comparative purposes. SIMS et al. (1997) estimated ages of 3–4 years for a 5 m long individual, and 8–15 years for 10 m long individuals, with sexual maturity at 6–9 m. Individuals of 11 m have also been reported (ALEXANDER 1998). Plotting these estimates next to those calculated from the foregoing work demonstrates a surprising agreement (Fig. 13). The sizes-at-age for each shark bracket those of *Leedsichthys*, suggesting that growth rate estimates for the Middle Jurassic osteichthyan do not appear to be unrealistically fast or slow when compared with those for modern-day large suspension feeding chondrichthyans.

Growth biology and ecology

The BERTALANFFY growth coefficient ‘K’ (PAULY 1994) produced for the plotted skeletal elements from *Leedsichthys* was no higher than 0.012 for any specimen. Although these figures may relate to growth of the element and not the whole animal, sharks and rays also grow at a slow rate, with $k=0.04-0.16$, tend to live long and attain large sizes, with dogfishes (*Squalus*), for example, having a lifespan up to 70 years (DAS 1994). Some actinopterygians can live longer than this (some species of sturgeon live up to 152 years; DAS 1994: 85). Most teleosts have a lifespan of 2–15 years, but some species of rockfish can live over 120 years (DAS 1994), with one estimate for *Sebastes aleutianus* being 205 years (BERKELEY et al. 2004).

The value of the K coefficient has a further ecological significance. In times of local ecological stress, large animals in oceans are less vulnerable to localised ecological changes, as they are more able to move elsewhere (e. g., BAKKER 1993) in contrast to their smaller (or freshwater, or terrestrial) counterparts. However, MUSICK (1999), in his work on ecology of long-lived marine animals, found that the BERTALANFFY growth coefficient K is a useful indicator of potential recoverability from excessive mortality events. In particular, where $K \leq 0.1$, the animals are particularly vulnerable (e. g., most chondrichthyans, some teleosts, and the cheloniid sea turtles, MUSICK 1999). Such animals usually have low fecundity, slow growth, and late maturity, and recovery from high mortality in a population might take decades (see also BENTON 1986).

Conclusions

Available specimens of *Leedsichthys* were selected and placed in a likely rank order of relative size based on the size of cranial elements common to more than one specimen (Table 1). Careful selection of postcranial elements for scaling resulted in reasonable size estimates (Table 3). Gill rakers and lepidotrichia were sectioned and counts of annuli were used to derive ages for the individuals (Table 2). All three methods produced congruent results, with the rank order of specimens agreeing with the order of the postcranially based size estimates, which in turn agreed with estimated ages derived from annular counts. Although examination of further material is needed, in particular material documenting growth in the first years of life, these methods demonstrate a consistent pattern of size and age among different specimens of *Leedsichthys* and from three different parts of their skeleton. The size and age estimates are compatible with what is known of the growth of large, modern-day, oceanic, suspension feeding chondrichthyans.

Although *Leedsichthys* appears to have grown to a remarkable size for a bony fish, its growth, both in terms of rate and extent, is broadly comparable with that of basking sharks and whale sharks today.

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Authors' addresses:

Jeff LISTON, Department of Natural Sciences, National Museum of Scotland, Chambers Street, Old Town, Edinburgh, EH1 1JF, Scotland; School of Earth Sciences, Wills Memorial Building, University of Bristol, Bristol, BS8 1RJ, England; and Division of Environmental & Evolutionary Biology, School of Life Sciences, College of Medical Veterinary & Life Sciences, University of Glasgow, Glasgow, G12 8QQ, Scotland; e-mail: jliston@nms.ac.uk

Michael G. NEWBREY, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0, Canada; e-mail: mike.newbrey@gov.ab.ca

Thomas James CHALLANDS, School of Geosciences, Grant Institute of Earth Sciences, University of Edinburgh, West Mains Road, Edinburgh, EH9 3JW, Scotland; e-mail: info@geovertical.co.uk

Colin E. ADAMS, Scottish Centre for Ecology & the Natural Environment, University of Glasgow, Rowardennan, Glasgow G63 0AW, Scotland; e-mail: colin.adams@glasgow.ac.uk

