The occurrence of the Middle Jurassic pachycormid fish *Leedsichthys*

Jeff Liston[1]

[1] *Division of Environmental & Evolutionary Biology, Faculty of Biomedical & Life Sciences, University of Glasgow, Glasgow, Scotland. e-mail: jliston@museum.gla.ac.uk*

ABSTRACT - A review of the occurrences of the Middle Jurassic pachycormid fish *Leedsichthys* is presented, including a new French locality. The variety of past misidentifications of these remains is noted, and the bones reinterpreted according to information derived from the broader hypodigm of material available for study. Trace fossils from the Lower Callovian outside Basel in Switzerland are assessed with regard to *Leedsichthys*, in addition to a review of relevant body fossil material from France, Germany and Chile.

Key words: *Callovian, Lexovisaurus, Pachycormidae, Atacama Desert, Kimmeridgian, Vaches Noire, Cap de la Hève, Ornatenton, Liesbergmüli*

Leedsichthys, **un poisson pachycormidé du Jurassique Moyen** - Les localités ayant livré des restes du poisson pachycormidé *Leedsichthys* du Jurassique moyen sont inventoriées, y compris une nouvelle localité française. Les diverses erreurs d'identification de ces restes sont notées, et les os sont réinterprétés selon les informations livrées par l'hypodigme élargi du matériel disponible pour étude. Des traces fossiles du Callovien inférieur des environs de Bâle, en Suisse, sont évaluées en relation avec *Leedsichthys*; un inventaire du matériel osseux pertinent provenant de France, d'Allemagne et du Chili est dressé.

Mots-clés: *Leedsichthys, Callovien, Lexovisaurus, Pachycormidae, Desert de l'Atacama, Kimméridgien, Vaches Noires, Cap de la Hève, Ornatenton, Liesbergmüli.*

INTRODUCTION

Although first described in 1889, a number of historical misidentifications of its bones have hindered the spread of awareness of the osteology of *Leedsichthys*, leaving this animal obscure. Of the few published works that have dealt with *Leedsichthys*, most have concentrated on material collected from the Callovian Oxford Clay around Peterborough. In this paper, some of the more commonly misidentified elements will be noted with reference to their likely position in the skeleton of *Leedsichthys*, with particular emphasis being given to material coming from localities outwith the vicinity of Peterborough in England. A summary of specimens referred to in detail is presented in the Annexe (Tables 1 and 2). This work is a prelude to a broader reassessment of all identified skeletal elements of *Leedsichthys*.

EARLY ENGLISH DISCOVERIES

Up to the time of the first discovery of *Leedsichthys*, the Callovian Oxford Clay around Peterborough (fig. 1) had yielded large reptile bones for many years (Porter, 1861), mostly through the endeavours of the fossil-collecting gentleman farmer Alfred Nicholson Leeds (Leeds, 1956). The fact that reptilian remains were known to be reasonably common, combined with the unusually large, thin and flat quality of a new set of bones, led to the first describer appending *Leedsichthys* bones to a description of some stegosaur bones from the same clay (Hulke, 1887). Hulke also incorrectly described the material as coming from the Kimmeridge Clay (Kimmeridgian in age, 154.7-152.1 mya), when it was actually from the older Callovian Oxford Clay (157.1-167.3 mya) around Peterborough (Harland *et al.*, 1990).

In attributing these fossilised remains to a stegosaur, the reasoning of Hulke was that these large plate-like bones resembled the armour plates described from the back of *Stegosaurus* from the Jurassic deposits of the Rocky Mountains of the United States by Othniel Charles Marsh (Marsh, 1880; 1881; 1887). The year after publishing his analysis of the dermal armour of *Stegosaurus* (Marsh, 1887), Marsh himself visited England. He had spent the previous ten years collecting large quantities of dinosaur material in the United States, and was now touring Europe to review all the dinosaur material he could track down, for comparative purposes (Marsh, 1889). Hulke's paper had attracted Marsh's attention, and he wished to examine the dinosaurian remains in Alfred Leeds' collection, including those identified as dermal plates of a stegosaur. The question, raised by Hulke (1887) was whether or not the Peterborough *Omosaurus* was congeneric with the North American *Stegosaurus*. Marsh travelled to the Eyebury home of the collector Alfred Leeds to see the material ('OC Marsh from Yale' is noted in the Eyebury visitors' book as visiting on 22nd August 1888, in the company of Henry Woodward, Keeper of the Department of Geology, British Museum (Natural History) (Anonymous, 1921)), and declared emphatically that the plate-like bones in question were in fact "piscine" in character (Smith Woodward, 1889a: p. 452). Such mistakes evidently continued to bother Marsh, as he wrote in his last letter to Henry Woodward, some ten years later, regarding some casts he was sending him: "… considering what confusion there seems to be in your country on the subject [of the Dinosauria], good casts of the characteristic American specimens might help on the missionary work of scientific instruction, and thus aid in bringing still nearer together our two countries." (Woodward, 1899). Although Hulke was in the wrong in his identification of those particular flat bones, he was at least partly in the right, as the other bones that he used in his description (not associated with the large flat plate-like bones) are still regarded as belonging to the stegosaurid *Lexovisaurus* (Hoffstetter, 1957).

At the time of Marsh's visit, Arthur Smith Woodward was a relatively new employee at the British Museum (Natural History) (Townsend, 1962), who specialised in fossil fish. Alerted to the piscine nature of this specimen, Smith Woodward gave early intimation in a review of the fossil record of sturgeons that a new fish was soon to be described, stating his belief that it was a large "Acipenseroid" (Smith Woodward, 1889b). However, the anticipated description was somewhat disappointing when it emerged in print (Smith Woodward, 1889a). Certainly, the reported sizes of the bones were impressively large, but their identifications were extremely vague and uncertain (Smith Woodward, 1889a), Smith Woodward later admitting that beyond the gill rakers and fin-rays, the true identities of the bones of this fish were still far from clear (Leeds & Smith Woodward, 1897).

Unsatisfactory though Smith Woodward's initial description of Alfred Leeds' specimens (the type BMNH P.6921 and the "doubtfully associated" BMNH P.6922) might have been, it did also note that the remains of this fish had also been found in the Callovian Vaches Noire of Normandie in France – specimen BMNH 32581 (fig. 2) (Smith Woodward, 1889a). In spite of this, Wenz omitted *Leedsichthys* from her 1967 faunal list of fossil fish that occurred in the Vaches Noire area between Villers-sur-Mer and Houlgate, mentioning only *Mesturus* and *Eurycormus* (Wenz, 1967). The distribution of *Leedsichthys* was clearly not restricted to the district of Peterborough, and indeed a 265mm long fin-ray fragment of *Leedsichthys* excavated from the Oxford Clay of Christian Malford (fig. 1), Wiltshire, had already been purchased by the British Museum (Natural History) from William Cunnington Esq. in February 1875 (BMNH 46355).

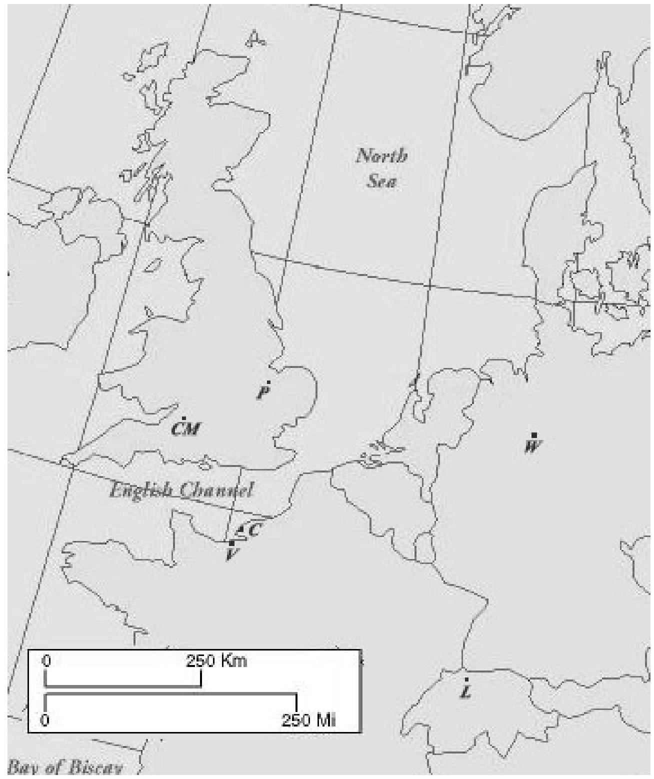


Figure 1 - Map showing European localities where *Leedsichthys* remains have been uncovered. C = Cap de la Hève; CM = Christian Malford; L = Liesberg P = Peterborough; V = Villers-sur-mer; W = Wiehengebirge.

FRENCH FINDS

The specimen from Vaches Noire (Dives, Normandie) noted by Smith Woodward (1889a) is a concretion 12cm across, containing around twenty disarticulated gill rakers ranging in length from 98-114mm (fig. 2). It was purchased by Richard Owen as part of "a series of specimens from the Jurassic of Normandie" from "M'sieu Tesson of Caen" in 1857, recorded as "Branchiostegous rays of Fish" (Palaeontology Department specimen catalogues, additions Geology, Vertebrata volume 2; NHM unnumbered; Buffetaut, 1983), and is the earliest known collected specimen of *Leedsichthys*. There has been a thriving culture of fossil collectors in the area between Villers-sur-Mer (fig. 1) and Houlgate for many years, to the extent that Flaubert referred to it in his posthumously-published novel 'Bouvard et Pécuchet'

Figure 2 - BMNH 32581, a concretion of disarticulated gill rakers from Vaches Noire, the earliest-collected specimen of *Leedsichthys*. Scale bar = 50mm.

(Flaubert, 1884) (noting, in the process, the reputation that the collectors of Villers had, of selling their specimens to the English). In this novel, the two main characters are retired, and develop an enthusiasm for collecting fossils. Almost prophetically, at one point Bouvard and Pécuchet believe that they have discovered a gigantic fossil fish in the Jurassic cliffs of Normandie (albeit at the Bajocian type locality of Falaise des Hachettes), but it is so fragile that they destroy it while attempting to retrieve it.

The tradition of private collectors on these beaches has continued to the present day: Bardet *et al.* (1993) used material collected recently by M & M Charles and G & E Pennettier for her histological analysis, which identified fossilised remains as belonging to *Leedsichthys*, and the Pennettiers still acquire well-preserved material (including *Leedsichthys*) from this site (Liston, 2008). The Callovian outcrop at this locality today is extremely poor. In the late nineteenth and early twentieth century, the ledges of Upper Callovian would usually become visible in the winter, but this has become rarer. At the start of the twentieth century, nearby excavations for a dam and local railway resulted in the sand level rising to cover the *Peltoceras athleta* zone.

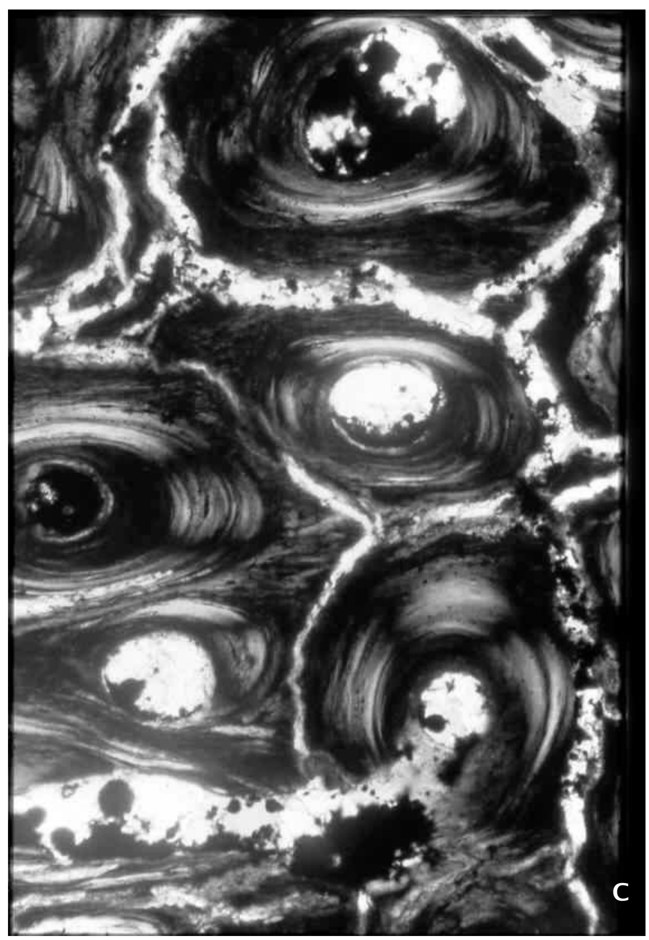


Figure 3 - Ceratobranchial of *Leedsichthys* from the collection of G. and E. Pennettier. A Ceratobranchial of *Leedsichthys* from the collection of G. and E. Pennettier, in dorsolateral view to show uncrushed form of bone. Scale bar marked in centimetres.; B Ceratobranchial of *Leedsichthys* from the collection of G. and E. Pennettier, sectioned to show uncrushed form of bone.; C Transverse section of ceratobranchial under microscope from the collection of G. and E. Pennettier, showing extensively remodelled lamellar bone. Image courtesy of N. Bardet.

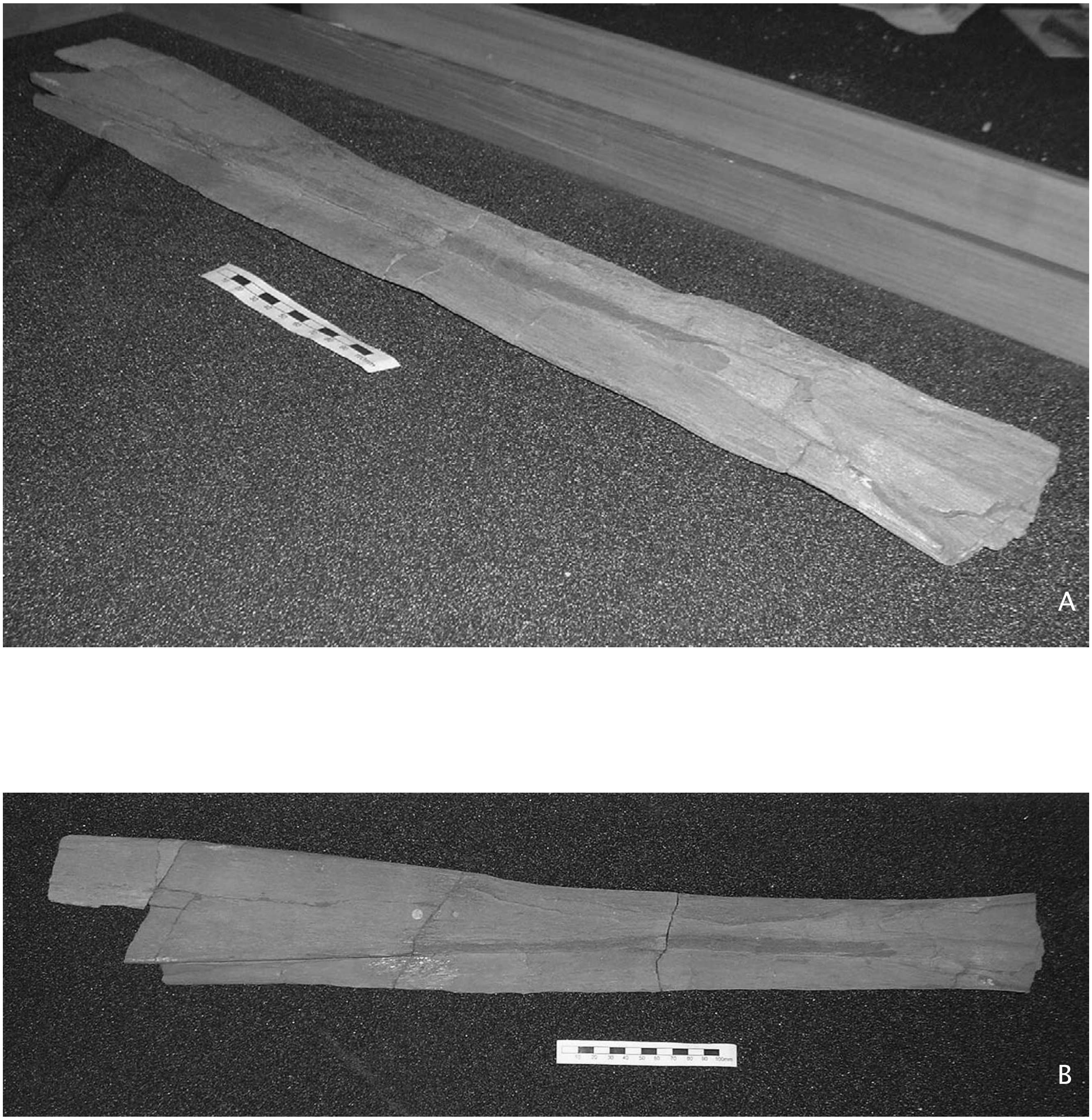


Figure 4 - Ceratobranchial of *Leedsichthys*, part of the holotype specimen BMNH P.6921. A Ceratobranchial of *Leedsichthys*, part of the holotype specimen BMNH P.6921, in dorsolateral view, to show flattening of bone. Scale bar = 100mm., B Ceratobranchial of *Leedsichthys*, part of the holotype specimen BMNH P.6921, in dorsal view. Scale bar = 100mm. C-Gill basket specimen BMNH P.10156 on display in the 1970s. This specimen was excavated as a nodule by Alfred Leeds, and so preserves much of its three dimensional form without the crushing normally associated with English Oxford Clay specimens of *Leedsichthys*. The hyomandibula on the left is 687mm high. Image supplied by Alison Longbottom, NHM (London).


HYOMANDIBULA AND GILL-ARCHES OF
SICHTHYS PROBLEMATICUS A.S. Woodward.
PETERBOROUGH.
P.10156.

C

The situation has slowly deteriorated over the decades since then: collectors today have to dig below the 0.5-1 metre thick sand at the foot of the Kimmeridgian-Toarcian Vaches Noire cliffs at low tide, under the constant threat of the imminent return of the tide. The fossil material yielded reveals not only the presence of *Leedsichthys*, but also a Callovian assemblage of pliosaurids, plesiosaurids and crocodilians, as diverse as that of the Oxford Clay around Peterborough. Although problematic to access, in many ways the material has advantages over the English equivalents, as it is usually well supported by internal sediment and so preserved in three dimensions (figs. 3a-c), rather than crushed flat (figs. 4ab). Some specimens occur in nodules, requiring hours of mechanical preparation, but the results are greatly enlightening in terms of the overall morphology of the undistorted bones.

In 2004 a new *Leedsichthys* locality (fig. 5) was discovered in the Argiles d'Ecqueville supérieur north of Octeville at Cap de la Hève (fig. 1), northeast of the Villers-sur-Mer Vaches Noire Callovian locality (D. Gielen, pers. comm., 03/2005). This is particularly important as it is an Upper Kimmeridgian occurrence (Gallois, 2005), and extends the stratigraphic range of this genus by 5 million years. The Kimmeridge Clay of Dorset was referred to as a source of *Leedsichthys* material by Arthur Smith Woodward (Smith Woodward, 1895; Leeds & Smith Woodward, 1897; Zittel, 1925) but with no record of where the relevant specimen(s) might have been deposited. No material matches this description within the collections of the Natural History Museum (London). It has been suggested (Martill, pers. comm.) that climatic change at the end of the Callovian (Dromart *et al.*, 2003a; 2003b) was responsible for driving *Leedsichthys* from the northern hemisphere via the Hispanic Corridor (Riccardi, 1991; Whatley & Ballent, 1994; Tethys Seaway of Arratia, 1996) so that after the Callovian the genus continued only in the southern hemisphere (see 'American Occurrences', below). However, it is clear from this occurrence in the Upper Kimmeridgian of France that if this constraint was in effect, then it was only a temporary restriction of the geographical range of *Leedsichthys*.

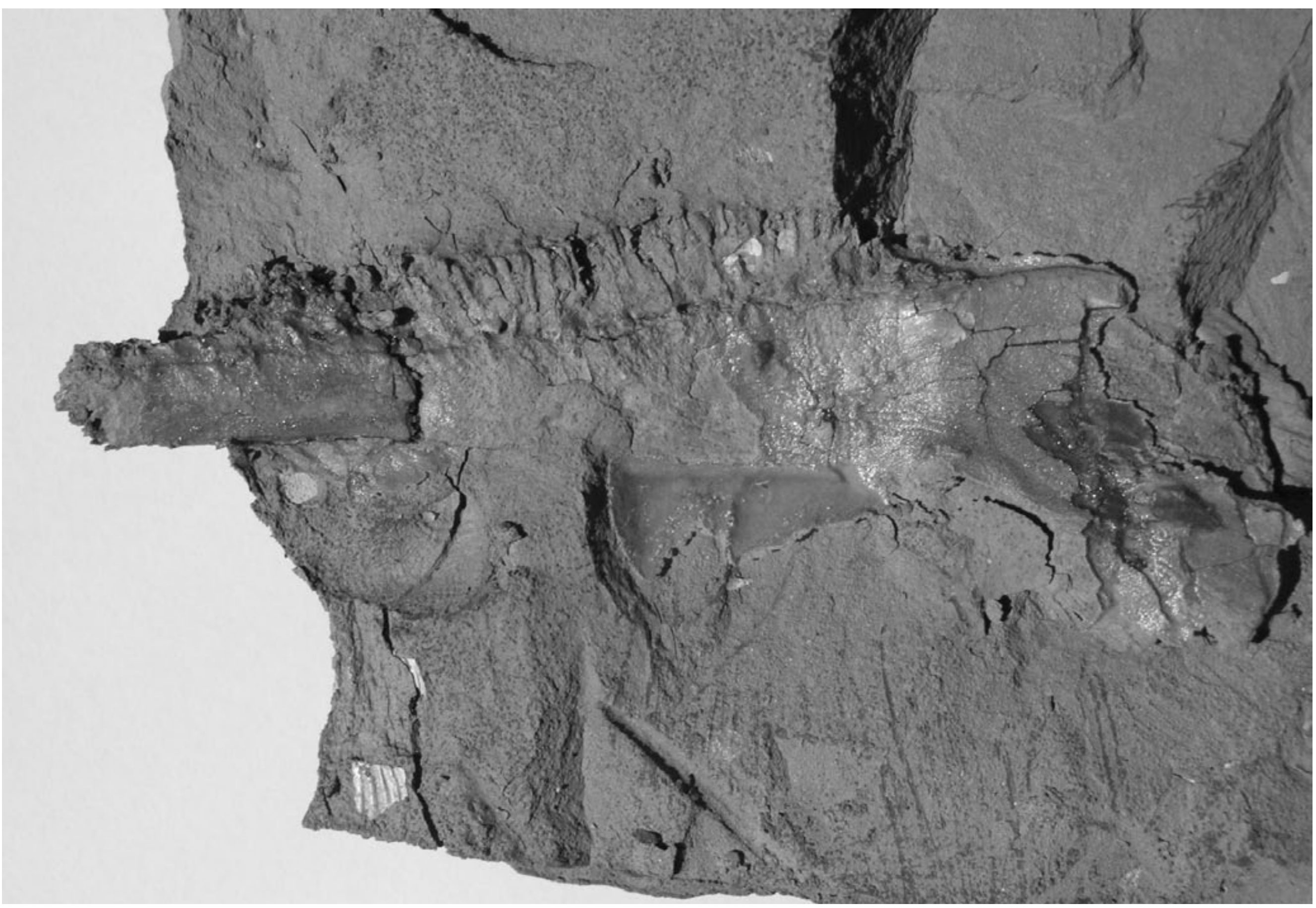


Figure 5 - Gill raker of *Leedsichthys* GLAHM 132787 from the Upper Kimmeridgian of Cap de la Hève, image courtesy of D. Gielen. Gill raker is 73mm in length.

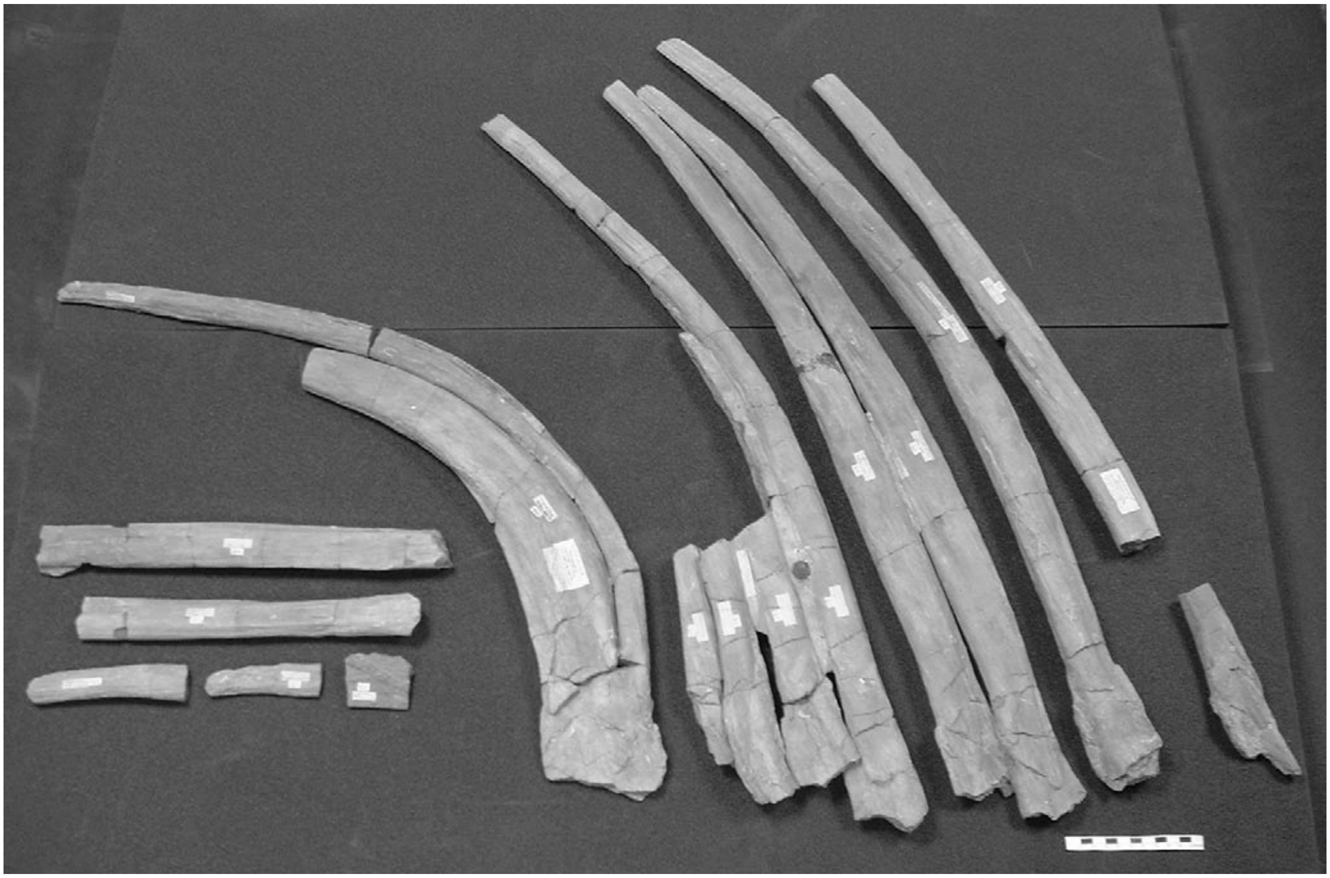


Figure 6 - CAMSM J46873, the *Leedsichthys* remains figured as stegosaur 'Schwanzstacheln' by von Huene in 1901. Scale bar = 100mm

'SCHWANZSTACHELN'

In 1901 Friedrich von Huene, of the University of Tübingen, Germany, visited the Woodwardian (now the Sedgwick) Museum of the University of Cambridge, to review possible dinosaur material held in the Cambridge collections (Huene, 1901). Following this visit, he published on a number of the specimens in the collection that he had interpreted as dinosaur material. Amongst these specimens was a series of associated bones that he figured as 'schwanzstacheln', or tail spines, of a stegosaurian dinosaur (specimen number CAMSM J.46873; fig. 6). The bones had been collected in 1899 by Henry Keeping, a rival collector to Alfred Leeds. Alfred Leeds had an arrangement with many of the quarrymen excavating the Oxford Clay in the pits around Peterborough, whereby he would financially reward them for notifying him of any bones they came across (Leeds, 1956). In order to get the quarrymen to give bones to him instead of Leeds, Keeping resorted to telling them that Leeds had stopped collecting bones (which he had not - Alfred Leeds continued to collect and prepare bones up until his death in 1917) (Leeds, 1956). Keeping had acquired the material examined by von Huene (1901) from clay brick pits in the Fletton district south of Peterborough – Alfred Leeds' prime collecting ground. Leeds was alerted to the erroneous identification by his friend Bernhard Stürtz of Bonn, who sent him a copy of von Huene's paper (1901). Leeds commented on the misidentification in a letter to Arthur Smith Woodward the same year, saying "I should like to have a cut at old Keeping – so as to expose his ignorance in putting these bones together – but it does not look as though any one at Cambridge knew much about bones." (Leeds, 1901).

The bones figured by von Huene (1901) are elongate and curved, extend up to a metre in length, and have a 'woven' surface texture common to many bones of *Leedsichthys*, in contrast to the conical and smooth-surfaced tail spines of a stegosaurian dinosaur (fig. 8d). In this specimen, through the hardening of the clay matrix into a concretion, something of the *in vivo* relationships of these bones seems to have been preserved (as noted by Huene [1901]). The bones have grooves down their basal lengths, so that they loosely interlink to form a longitudinal base. This sequence of curved elongate elements strongly suggests skeletal components of a meristic series. Possible candidates for such a series in the skeleton of an osteichthyan would be branchiostegals, supraneurals, neural spines, pleural ribs, haemal spines and dorsal fin-rays. Typically there are between thirty and fifty filiform branchiostegals in pachycormids (McAllister, 1968), and the bones figured by von Huene are neither the correct shape nor present in large enough numbers for these to be likely branchiostegals. Although it is possible that these elements are supraneurals, their curvature runs counter to that seen in other pachycormids, travelling superiorly then posteriorly, as opposed to posteriorly then superiorly (Smith Woodward, 1916; Hauff & Hauff, 1981), making these unlikely to be homologous bones to supraneurals. It seems unlikely that pleural ribs would articulate together, and the relatively swift change in curvature and length of these bones over the distance represented by CAMSM J.46873 would seem to argue against their being ribs or haemal spines, as they would seem to define a shorter fish like *Mola*, unlikely to be combined with such an extensive lunate tail as BMNH P.10000. Although different to the dorsal fin-rays of many osteichthyans, these bones are similar to the unsegmented form seen in other pachycormids such as *Asthenocormus* and *Saurostomus* (Smith Woodward, 1916; also specimen JM SOS 3556 which has a fracture running between the two sets of hemitrichia).

Hoffstetter (1957) correctly noted that the bulk of the specimens figured by von Huene (1901: fig. 3) were of a giant fish, rather than a stegosaur (Hoffstetter, 1957: p. 542). Unfortunately Galton (1985), in relaying Hoffstetter's 1957 correction to von Huene's misidentification, referred to these bones as gill rakers. Contra Galton (1985), they resemble the dorsal fin spines (rather than metre long gill rakers) of pachycormids like *Asthenocormus* (pers. obs.) from the Tithonian Solnhofen limestone and *Saurostomus* from the Toarcian Holzmaden shale. A similar view was espoused by Alfred Leeds in a personal letter to Arthur Smith Woodward (The Official Archives of The Natural History Museum, held by the General Library (NHM-GL) and Earth Science Library (NHM-ESL); Alfred Nicholson Leeds to Arthur Smith Woodward, 18 March 1898; Correspondence section NHM-GL DF 100/31(Liston & Noè, 2004)). Also, many specimens of *Leedsichthys* contain this type of elongate and curved bone (GLAHM V3363, PETMG F1, PETMG F174, PETMG R189, OUMNH J.1803, NMW 19.96.G9, CAMSM X.50111, CAMSM X.50117, CAMSM J.27444, CAMSM J.46876-8, LEICT G471.1897, LEICT G472.1897, LEICT G473.1897, LEICT G519.1993.1-7, BMNH P.6921, BMNH P.6924, BMNH P.6925, BMNH P.6928, BMNH P.11825, BMNH P.66341, BMNH P.66342), although rarely do they contain such an apparently complete sequence as that represented by the Cambridge specimen.

The other specimens figured and described by von Huene in his 1901 paper on dinosaur material from the Woodwardian (now Sedgwick) Museum did actually constitute stegosaurian and other dinosaur remains. But such mistakes have been common since *Leedsichthys* was first described. Specimens sold to Liverpool University in April 1919 by the Leeds Family as *Leedsichthys* were later erroneously described as bones from the skull roof of the ichthyosaur *Ophthalmosaurus icenicus* and ribs from indeterminate reptiles (Neaverson, 1935). Lack of awareness of this fish and the nature of its remains have also frequently led to misidentifications of some of the more obscure remains of other animals, as being components of *Leedsichthys*. In one case, the misidentification of some small actinopterygian jaw bones as the gill rakers of *Leedsichthys* led to this fish erroneously being reported as occurring in the Kellaways Sands of Lincolnshire (Brown, 1990; Brown & Keen, 1991). In another case, a beautifully complete specimen of a pliosaur exoccipital-opisthotic was misidentified as (presumably) being a vertebra of *Leedsichthys* (Noè *et al.*, 2003), although due to reduced ossification of its skeleton (Liston, 2004a), no vertebra has ever been recovered for *Leedsichthys*. This is a phenomenon that varies widely across the Pachycormidae, from the centra being well preserved in a small genus like *Haasichthys* from the Toarcian of Luxembourg (Delsate, 1999), to the centra being utterly absent in large Toarcian specimens of *Saurostomus* (Smith Woodward, 1916) and *Ohmdenia* (Hauff, 1953; Lambers, 1992). The preservation of vertebral components can also be seen to vary widely even across different species of the genus *Pachycormus*, excavated from the Toarcian of Holzmaden (Hauff & Hauff, 1981).

GERMAN OCCURRENCES

Almost a century after the first description of *Leedsichthys*, the geographical distribution of this taxon expanded, with a specimen found in northern Germany, in the Störmer quarry of Wallücke (fig. 7a), in the 300 metre high chain of the Wiehen Mountains ('Wiehengebirge') between Osnabrück and Minden, near Bünde. In 1978, a school-age group of amateur palaeontologists from the Scientific Club for Bielefeld and District (Naturwissenschaftlicher Verein für Bielefeld und Umgegend), collecting ammonites (fig. 7c), found the first bony remains from this site – pliosaur bones lying just below the *Erymnoceras* sp. layer that they were collecting from. Over time, as they collected more of these ammonites from the Middle-Upper Callovian strata of the 'Ornatenton' (as the Oxford Clay is referred to in this region), more of the bone-bearing layer was exposed, until in July 1982 the first remains of *Leedsichthys* were recovered. In the same month, another school-age group of collectors, from the Bünde Palaeontological Working Group (Paläontologische Arbeitsgruppe Bünde) independently found the remains of the same fish at the site. But it would not be until six months later that a chance encounter between members of each group (Ralf Metzdorf of the former, and Matthias Metz of the latter) in an entirely different quarry led to the realisation that each group had been excavating the same animal.

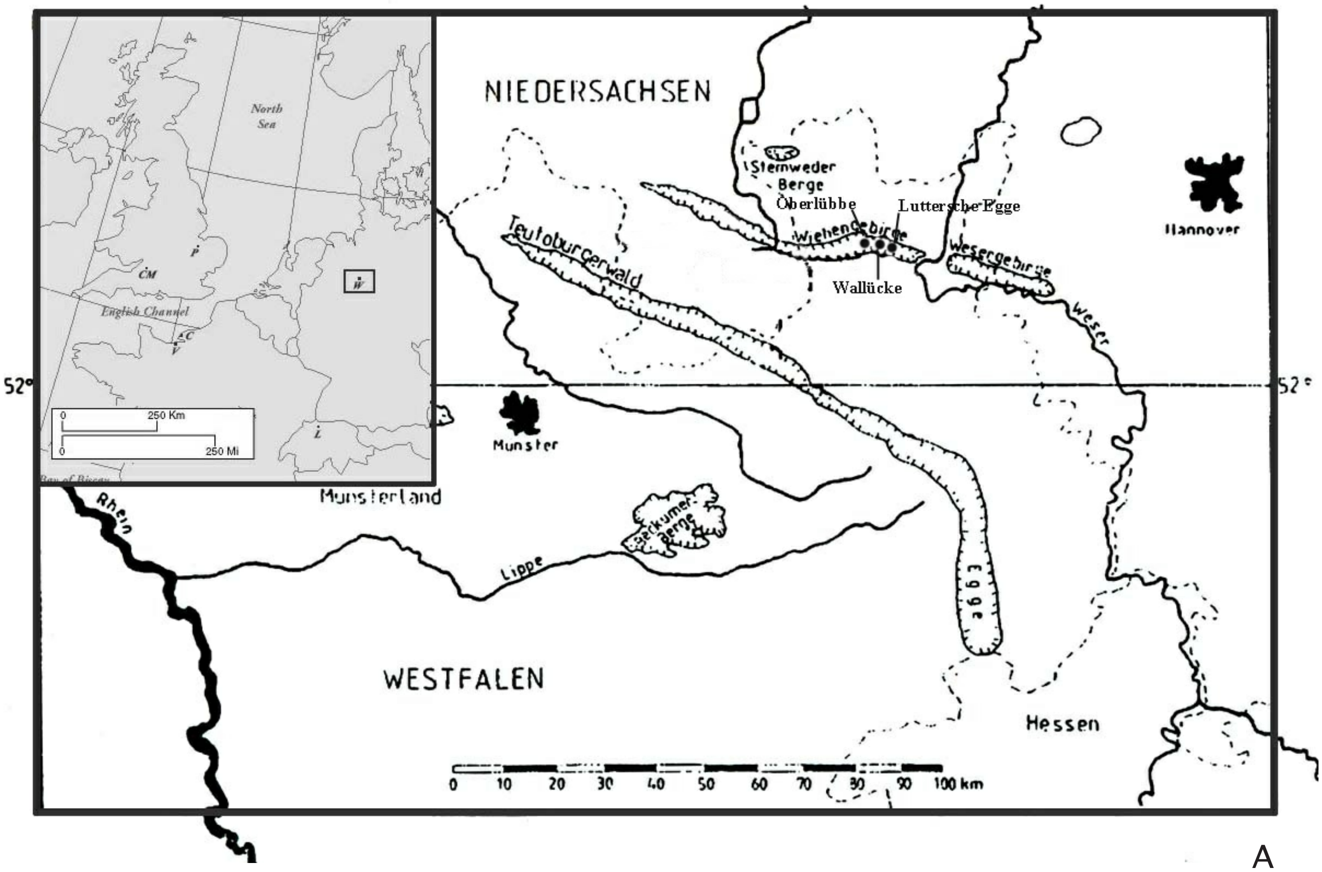
In the meantime, the Bielefeld group had brought their finds, resembling fossilised reeds, to Martin Büchner of the Bielefeld Natural History Museum for identification. Although he could not say to what animal they might have belonged, he believed them to be vertebrate and therefore potentially important, and so arranged for them to be passed to the Office for the Protection of Monuments. The representative from the Office, Mr Niemier, decided that they were fossil plant, and sent Mr. Schultka of the Palaeobotany Research Group of the Westfalian Wilhelms-University to the quarry to collect a sample for analysis. Büchner and Schultka independently thin-sectioned the material and confirmed the original analysis – that it was indeed bone, and not plant material, as Haversian systems appeared to run through it, but no phloem or xylem vessels (fig. 7di and dii).

Following the chance meeting of Metz and Metzdorf, and the results of the histological analysis, a joint excavation was planned by both groups of collectors, running from November 1st to 3rd 1983 (fig. 7b). This yielded a large number of vertebrate remains (which mainly were transferred to the Westphalisches Museum für Naturkunde, although some pieces entered private collections), spread over an area roughly 30 metres by 30 metres. As a result of this, three further digs were conducted on the same site between 1985 and 1989 by the Westphalisches Museum für Naturkunde, each unfortunately only yielding relatively few remains in comparison with the November 1983 excavation. The last of the three digs reported only finding "a few bone splinters of the previous skeleton…badly eroded by weathering." (Probst & Windolf, 1993: p. 157). The vertebrate remains from all of these digs were almost entirely *Leedsichthys*, the only exceptions being pliosaur material and chondrichthyan teeth. Importantly, this Störmer specimen was the first to ever be mapped (Probst & Windolf, 1993; Michelis *et al*., 1996), albeit retrospectively, by Metzdorf, using photographs taken over almost fifteen years. This provided the first indications of the relative disposition of the bones of a specimen of *Leedsichthys*, as all previously collected specimens had either been accessioned as isolated and unconnected slabs, or had had all matrix removed from them.

In 1986, Metzdorf prepared some of the material in the Westphalisches Museum für Naturkunde and took samples to Dr Rupert Wild of Stuttgart Natural History Museum, who identified one bone (WMfN PM 17006/8) found in the centre of the *Leedsichthys* assemblage as the 'schwanzstacheln' or tail spine of a stegosaurian dinosaur (fig. 8a). This was despite the fact that WMfN PM 17006/8 is a form of bone that is commonly found in other specimens of *Leedsichthys* from Peterborough (pers. obs.) (GLAHM V3363 (fig. 8b), PETMG F2, PETMG F174, PETMG R189, NMW 19.96.G8, CAMSM X.50118, CAMSM J.27438, CAMSM J.67471, LEICT G418.1956.15.2, LEICT G418.1956.15.5, BMNH P.6921, BMNH P.11823), and possesses a different surface texture, cross-section and no taper, compared with a stegosaurian tail spine (fig. 8d).

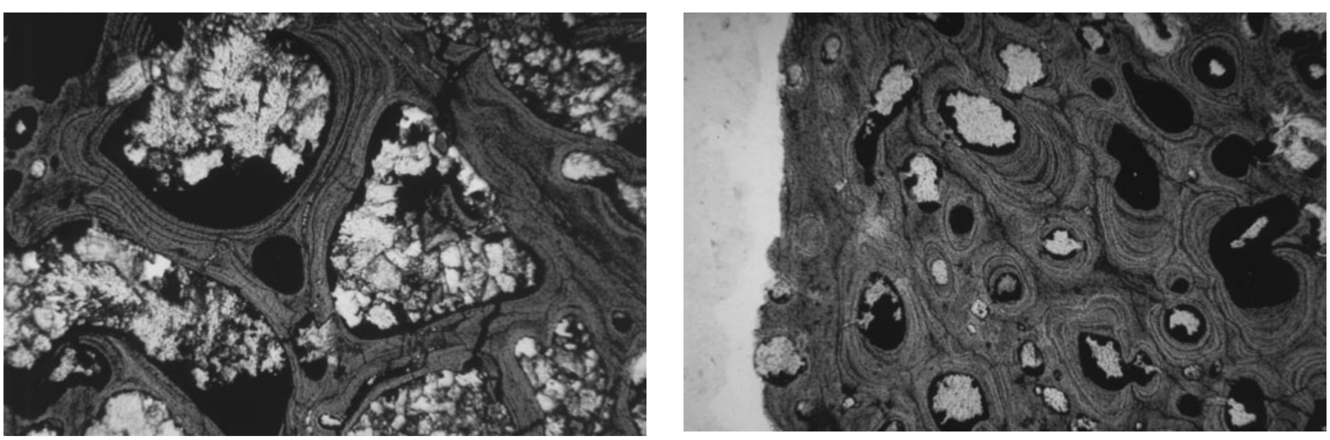
It should be emphasised that this is a completely different element to the bone misidentified by von Huene as a 'schwanzstacheln' some 80 years earlier (Huene, 1901). The tail spines of *Lexovisaurus* are three dimensional solid cones, with an extremely smooth external surface, whereas WMfN PM 17006/8 is hollowed and commonly presents as crushed in other specimens of *Leedsichthys*. This bone is a hypobranchial, from the anterior part of the gill basket of *Leedsichthys*. As well as the crushed material listed above, this identification can be confirmed by comparison with the uncrushed hypobranchials present in the articulated gill basket specimen BMNH P.10156 (fig. 4c). This identification was supported during the June 2002 excavation of the most complete specimen of *Leedsichthys* (PETMG F174) yet found, jointly organised by the University of Portsmouth and the University of Glasgow's Hunterian Museum (see Liston, 2006). The initial identification of the possible presence of a specimen of *Leedsichthys* in the brick pit near Peterborough was made through a fragment of a bone that was a mirror image of one of the dorsal fin-rays figured by von Huene as 'schwanzstacheln'. After more than ten weeks of digging, consisting of 3,119 hours of fieldwork, more than 2,100 bones from the specimen (nicknamed 'Ariston', because it went 'on and on') had been retrieved. Amongst them was the bone morphotype identified at the Wallücke site as being a *Lexovisaurus* 'schwanzstachel', medial to the body end of a pectoral fin (fig. 8c), in the midst of other branchial elements and a dense mass of gill rakers. The Wallücke hypobranchial (WMfN PM 17006/8) is still displayed in the Westphalisches Museum für Naturkunde under the incorrect description of *Lexovisaurus* 'schwanzstachel'.

The misidentification of the isolated bone as stegosaurian was unfortunately consolidated in print by the publication of the results of a Masters Project in 1996 (Michelis *et al.*, 1996), which also created new levels of confusion by attempting to set out a histological means of distinguishing between the 'stegosaurian' bone and the bones of *Leedsichthys*, and proceeding to thus formally amend the diagnosis of the taxon. The bulk of the *Leedsichthys* bone morphologies retrieved from Wallücke are highly fragmented branchial arch elements and caudal fin-rays. One piece, WMfN PM 17006/1 (incorrectly figured in Michelis *et al*. (1996) as WMfN PM 17005/1 in Abb.5 the 'find-plan' map; in addition, WMfN PM 17005/2 is incorrectly noted in Michelis *et al*. (1996) as WMfN PM 17006/1 in Plate 2 Figure g), is a 470mm long section of fin-rays that appear to exceptionally show tendons linking parallel rays (fig. 9a). Apart from small fragments, the only significant dermal skull material is represented by WMfN PM 17005/23 (fig. 9b) and WMfN PM 17005/24 (fig. 9c). These two pieces are part and counterpart, with what appears to be a skull roof bone on WMfN PM 17005/23 impacted on to parts of the opercular series on WMfN PM 17005/24 (fig. 9d). Another bone of interest is specimen number PHB W 138/4 (Breitkreutz private collection): in a similar error to Galton (1985), Michelis *et al*. (1996) notes this as a gill raker, and illustrates it with a scale bar indicating a total size of around 75mm. In actuality, this is incorrect as the illustrated specimen is in fact 310mm long (the scale bar is incorrectly noted at 25mm, when it is actually 100mm), and not a gill raker, but a fragment of a left cleithrum. Although this specimen (fig. 9e) is similar to the 480mm long object figured in Abb.12 (PMM 19.1-21.1, 23.1 (fig. 9f)), it is likely that this latter object is a component of the lower jaw, possibly the supraangular, although a fi-


NIEDERSACHSEN
North Sea
English Channel
250 Km
250 Mi
Sternweder Berge
Oberlübbe
Luttersche Egge
Wiehengebirge
Wallücke
Wesergebirge
Weser
Teutoburgerwald
Hannover
Munster
Munsterland
Rhein
Lippe
Egge
WESTFALEN
Hessen
52°
0 10 20 30 40 50 60 70 80 90 100 km

A

B



D

Figure 7 - A – Map showing localities in the Wiehen Mountains in northern Germany, after Metzdorf. B - The November 1983 joint excavation in Wallücke. C - Bones of *Leedsichthys* exposed next to a specimen of *Erymnoceras*, the ammonite that originally led the fossil collectors to prospect in the quarry. Brick hammer for scale. D – Transverse sections of specimen by Büchner, showing no xylem and phloem vessels. B, C and D courtesy of R. Metzdorf.

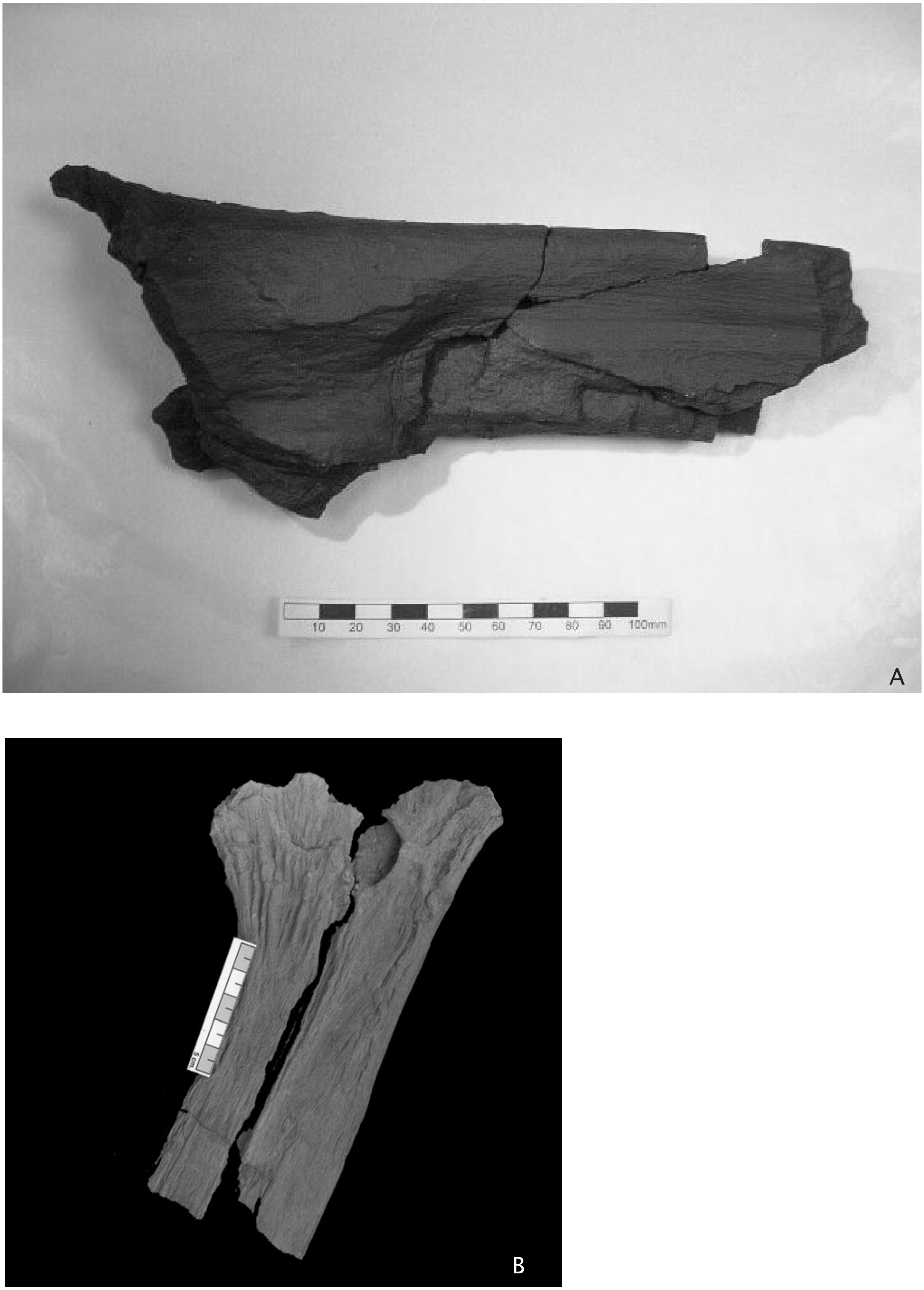

10 20 30 40 50 60 70 80 90 100mm
A
B

Figure 8 - The hypobranchials of *Leedsichthys*. A - Cast (GLAHM 109508) of WMfN PM 17006/8 Scale bar = 100mm B – Equivalent bone from *Leedsichthys* specimen 'Big Meg' (GLAHM V3363) Scale bar = 50mm; C - Equivalent bone from *Leedsichthys* specimen 'Ariston' (PETMG F174) indicated by black arrow. Boot in foreground for scale.; D Tail-spine of *Lexovisaurus* (CAMSM J46879) with element from series figured by von Huene (CAMSM J46873). Scale bar = 100mm.

nal identification has not proved possible. The same element is represented in BMNH P.66340 (which features the only dentary of *Leedsichthys* known) and the ventral gill basket specimen (BMNH P.10156/3). The fact that this element is only found with these two specimens (which predominantly represent the skeleton of the lower jaw area), and that only the dentary is known from the lower jaw ramus, is why it is suggested that this bone is a lower jaw element. It is worth noting that in the absence of any gill rakers with the Wallücke specimen, these elements with the fin-ray fragments are the only osteological link between these fossil remains and other specimens of *Leedsichthys*.

Although the description of much of the material from this quarry was correct, the spurious allocation of a bone to *Lexovisaurus* was indeed wrong – and having so correctly identified the rest of the bones, it is hard to understand why this morphology was allocated to a dinosaur completely unknown from the locality. Fragments of this German specimen of *Leedsichthys* are still cropping out today at the same site (pers. obs.). In 2002, pieces were collected (GLAHM 109518) and sampled for growth ring information, from which an estimated age of seventeen years, and a standard length estimate of around 7 metres have been derived (Liston, 2007). The remains of *Leedsichthys* have also been reported from the same stratigraphic level in a neighbouring quarry in the Wiehengebirge – Luttersche Egge (pers. comm. Metzdorf). But the Wallücke specimen itself, through a combination of different independent collecting activities and protracted weathering out over a number of years from a 40 degree inclined 900 square metre area, has become spread throughout a series of different public, as well as private, collections.

EVIDENCE FOR OTHER POSSIBLE EUROPEAN OCCURRENCES

Although no hard fossils of *Leedsichthys* have been identified in Central Europe, some Callovian age 'Rinnen' or 'gutter' traces uncovered in the Liesbergmüli clay pit (fig. 1, 20 km SW of Basel, Switzerland) in 1987 have been interpreted as 'feeding troughs' formed by large marine vertebrates preying on invertebrates inhabiting *Rhizocorallium* surface burrows (fig. 10a) in less than ten metres water depth (Geister, 1998). Geister interpreted the largest (in terms of both length and width) of these (figs. 10b-c) as being produced by pliosaurs, a conclusion rejected by Noè (2001) on the grounds that it would be physically impossible for a pliosaur to manoeuvre its head to generate the troughs without breaking its neck.

Geister specifically dismissed *Leedsichthys* as a potential manufacturer of these furrows, on the grounds that it was a filter feeder, but this is far from an obstacle. Geister proposed *Lepidotes*, *Asteracanthus* and *Heterodontus* as possible candidates for creating the narrower traces, arguing that there was a requirement for any candidate to have durophagous (crushing) dentition, but there are contemporary models for this type of feeding behaviour without such teeth. The recent *Heterodontus* can pump water and sand across its gills in order to expose prey hidden in the surface of the seabed. The recent freshwater fish, the Siberian sturgeon (*Acipenser baeri*), ingests large amounts of sediment and detritus while feeding on its benthic prey (chironomid larvae, amphipods, isopods and polychaetes) (Sokolov & Vasil'ev, 1989). Traces of such invertebrate fauna are commonly found in Callovian and Oxfordian marine sediments (e.g. Radwańska, 2004). Although previously the paddlefish has been cited as a 'benthic siever' in this style, Grande and Bemis (1991) have recently questioned whether this behaviour has actually been observed, or simply assumed from the unusual cranial morphology of these bony fish. Jobling (1995) also alludes to pleuronectids employing 'suctorial feeding' on benthic prey, but does not indicate the degree to which sediment is taken into the mouth, or further ingested by the body, during this process. Another recent suspension feeding fish *Abramis brama* (van den Berg *et al.*, 1992) derives 50% of its nutrition from zooplankton extracted from the water column through suspension feeding with its well-developed gill raker system, and 50% from chironomid larvae on the bottom of the lakes that it inhabits, although it bears edentulous jaws.

There are also marine, if non-piscine, examples of similar iliophagous behaviour, which are more comparable in terms of the size of the predator involved in extracting invertebrate prey from the surface sediment of the sea bottom. Murray *et al*. (2002) reviewed the largescale impact of such activities by a range of vertebrates. Hans Nelson and Johnson (Hans Nelson & Johnson, 1987; Hans Nelson *et al.*, 1987) have noted the production of channels similar to Geister's 'feeding troughs' in seafloor sediments at depths of 30-50 metres by California grey whales and Pacific walruses. The furrows created by Pacific walruses (*Odobenus rosmarus divergens*) are the results of the walrus hydraulically clearing the mud from clams detected in the sediment with its vibrissae. The walrus then sucks the clam from its shell. In contrast, the California gray whale (*Eschrichtius robustus*) feeds by sucking in large quantities of sediment containing the tube mat of the amphipod crustacean *Ampelisa macrocephalus*, which it then separates from the surrounding sediment, using its baleen plates. Like *Abramis brama*, the California gray whale also feeds on organisms that live in the water column. Although neither is a precise model for a trough generated by the predator's head ploughing a furrow in the sea bed, as Geister interprets the Liesberg traces, they establish the precedent of large marine vertebrates taking mouthfuls of fauna-rich sediment from the sea floor, in order to extract epibenthic invertebrates for ingestion, in a manner capable of generating large-scale feeding trails. It can be envisaged that this might be a form of feeding that a fish would grow into, through ontogenetic changes altering its range of prey and feeding styles (Jobling, 1995) in the same way as the feeding habits of any fish change with growth, as the feeding structures within the mouth attain an effective size to deal with extraction of prey from sediment.

So, far from being unreasonable for a suspension feeding animal to generate these troughs, there are plenty of contemporary examples of a wide range of suspension-feeding vertebrates indulging in this behaviour. Given the quantity of marine vertebrates today that can facultatively utilise this benthic food source, it would be surprising if such a vertebrate did not occur in the Callovian marine ecosystem. There is nothing in the anatomy of *Leedsichthys* to contraindicate such a feeding strategy, and van den Berg *et al*. (1994) specifically suggested that interdigitating gill rakers of the form displayed by *Leedsichthys* indicates a facultative suspension feeder that could vary its interraker gap in order to change its diet from benthic to suspension feeding and back again. It may have been that feeding on benthic invertebrates was the preferred feeding strategy for *Leedsichthys* when a suitably rich source of plankton was not immediately available. Geister's (1998) argument that these troughs are biologically generated is convincing, the troughs are wide, the margins smooth, orientation meandering (like those formed by Pacific walruses on the Bering Shelf, Hans Nelson & Johnson, 1987) or straight. Reviewing the recognised Callovian marine fauna, and excluding the pliosaurs on the biomechanical grounds suggested by Noè (2001), leaves *Leedsichthys* as the only currently known candidate to have a gape large enough (up to 600mm in width) to generate such a trough in the fashion suggested. These widest troughs (Geister's gutter-type 'c') are also the ones that can exhibit a sinusoidal trough pattern (rather than the straight lines of the other gutter traces), perhaps reflecting the regular lateral oscillation of a swimming body travelling in anguilliform or carangiform mode (Blake, 1983), rather than random movements or foraging behaviour. But this is all at best circumstantial evidence, and in the absence of any body fossils to support arguments for the presence of this fish in this environment, this model remains conjecture.

The marine Callovian outcrops further east in Europe, noteably in Poland and south-east of Moscow, but thus far no report of *Leedsichthys* has been made from these regions. A 70mm-diameter fish vertebra has been reported from Poland's marine Callovian (A. Radwanski, pers. comm. 2004), but as no vertebrae have ever been identified from *Leedsichthys*, this find is unlikely to belong to that fish. As noted before, *Leedsichthys*, like some other members of the Family Pachycormidae, appears to exhibit a trend towards non-ossification of this part of its skeleton. As such, this vertebra is more likely to belong to a large example of a caturid like *Osteorachis* (known from the Peterborough Oxford Clay; Martill, 1991) than to *Leedsichthys*.

REMAINS FROM THE AMERICAS

In terms of sedimentary marine units that might represent an appropriate environment for an animal such as *Leedsichthys*, the North American Sundance Formation seems a likely candidate. The Callovian-Oxfordian range of the Formation (Uhlir *et al.*, 1988; Weems & Blodgett, 1996) neatly encompasses the range of the fish, as described earlier. Although parts of the formation represent a shallower environment than the Oxford Clay (Uhlir *et al.*, 1988), it has proven to be a deep enough marine environment to be a source for large marine vertebrate remains (Knight, 1898; Weems & Blodgett, 1996). As such, it might be considered surprising that the remains of *Leedsichthys* have not yet been identified within this Formation, but it has been argued that the marine reptiles occurring in the Sundance Formation exhibit an apparent provincialism that indicates a possible discrete Late Jurassic biogeographic Boreal Realm (Weems & Blodgett, 1996). If this reflects a geographic or environmental separation between the Middle-Upper Jurassic European and western North American assemblages, then it would not be surprising for this constraint to also have applied to a large fish such as *Leedsichthys*.

However, the remains of *Leedsichthys* are not simply constrained to Europe: although the Jurassic of North America has not yet yielded any remains, the Jurassic (Oxfordian, 157.1-154.7mya) of South America has. Alexander Andrew Fergusson Leeds (or 'Fergie' as his family called him), the eldest son of Alfred Leeds (the original discoverer of *Leedsichthys*), worked for the copper miners Norman Walker & Co. in Antofagasta in Chile (fig. 11a) from 1897 until 1903. By a somewhat bizarre coincidence, in August 1978 in the archaeological museum of this same city on the western edge of the Atacama Desert, Hans-Peter Schultze (of Lawrence University) came across the remains of a large fish (figs. 11b-c) from the local Middle Jurassic. Brought into the Museo de Arqueologia over the previous five years, the remains seemed to represent extremely large gill rakers within a limestone matrix. Although, like Arthur Smith Woodward's first provisional identification (Smith Woodward, 1889b), they were marked as possibly being part of a large acipenseroid/chondrostean fish, they were in fact the remains of *Leedsichthys* (Arratia & Schultze, 1999). On chancing upon them in the Museo de Arqueologia, Antofagasta, Hans-Peter Schultze organised a dig, which retrieved more *Leedsichthys* material from Quebrada San Pedro and Quebrada Aquada Chica for this museum (fig. 11d). In March 1994 at a nearby locality north of Quebrada del Profeta, he discovered and excavated a new and extensive specimen embedded in an extremely large block of limestone matrix (fig. 11e) (Arratia & Schultze, 1999) over several days with pickaxes and shovels. Like the other Atacama material, this specimen preserves detail well, but the remains are less robust than the matrix surrounding it, making preparation difficult. The Quebrada del Profeta 1994 material (Museo Nacional de Historia Natural, Santiago) is preserved in nodules, and has yet to be fully prepared for analysis. Its extensive nature (filling several crates) indicates a specimen that has much valuable information to contribute about the anatomy and lifestyle of this remarkable animal, in particular the structure of its gill basket. Shortly after this excavation, Martill and Frey were presented with a specimen of what was thought

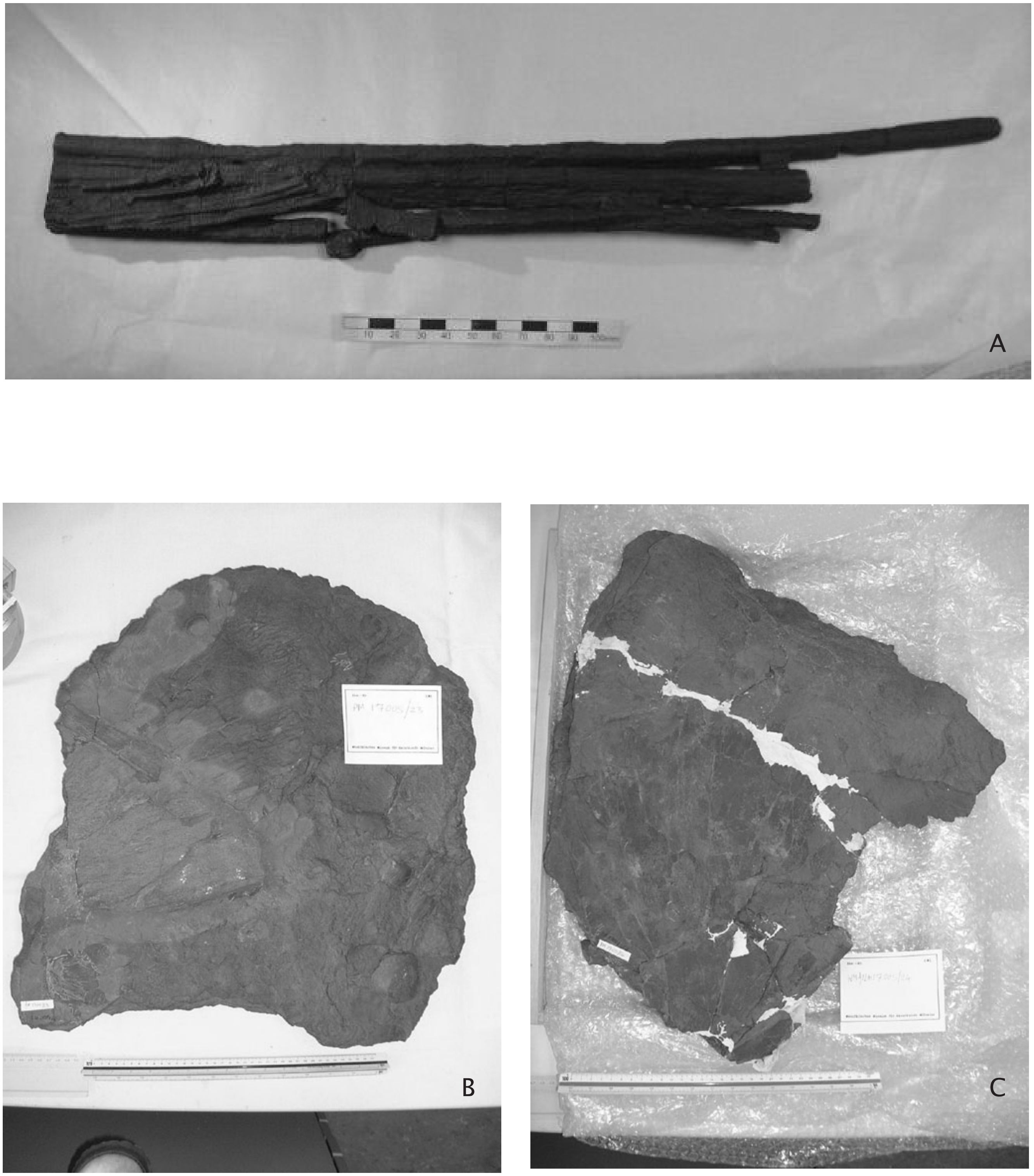


Figure 9 - A – Cast (GLAHM 109509) of WMfN PM 17006/1, showing apparent tendons cross-linking between fin-rays Scale bar = 100mm.; B - Skull roof element WMfN PM 17005/23. Scale bar below is 300mm. and C - Opercular element WMfN PM 17005/24. Scale bar below is 300mm. D - WMfN PM 17005/23 and WMfN PM 17005/24 as found in the field. Brick hammer for scale. E - PHB W 138/4 with PMM 19.1-21.1, 23.1 Brick hammer for scale. ; F - PMM 19.1-21.1, 23.1 as found in the field. Brick hammer for scale. D and F courtesy of R. Metzdorf.

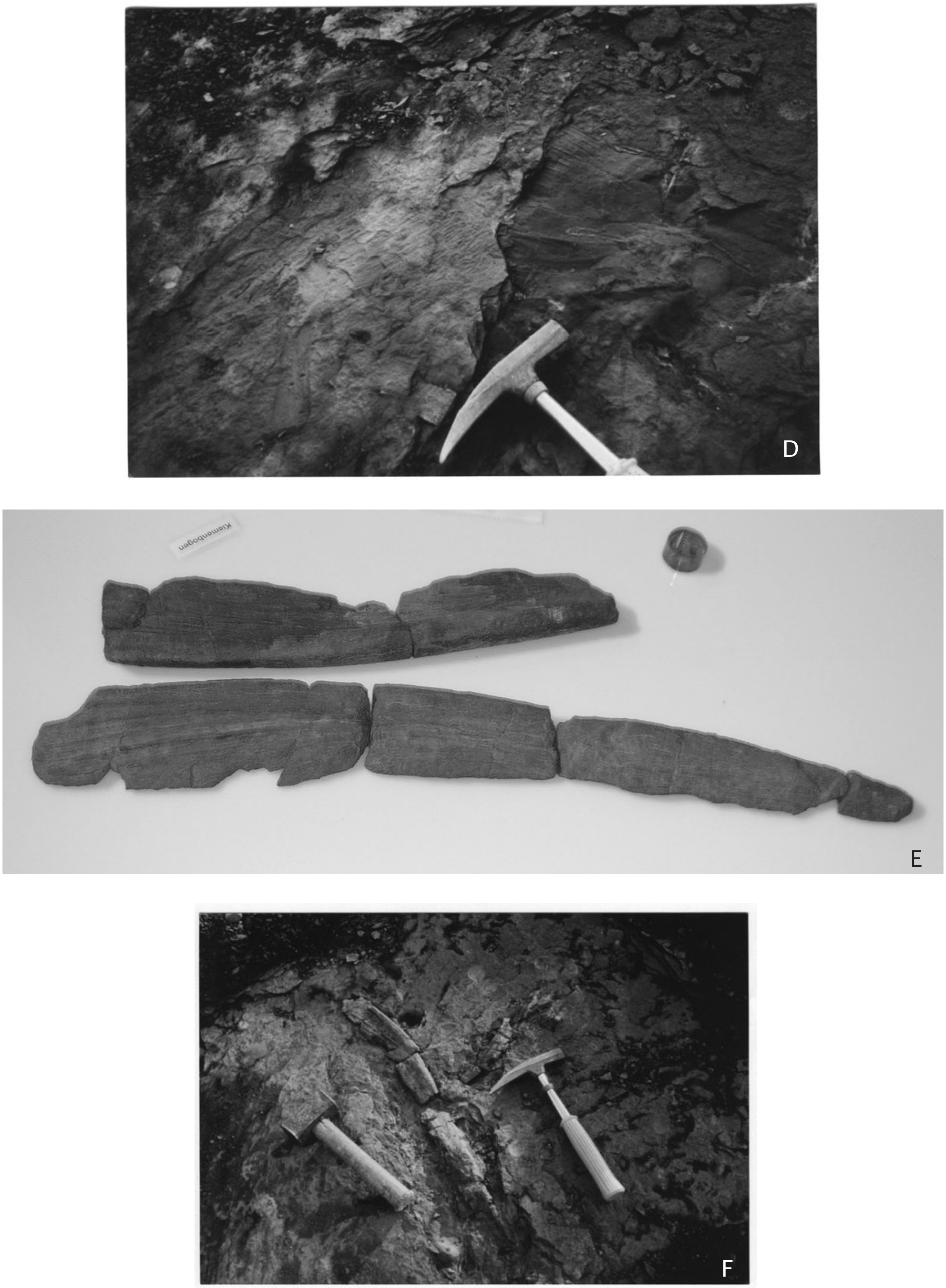

D
Kiemenbogen
E
F

Figure 10 - A – The Liesbergmüli clay pit in 1987, showing the range of alleged iliophagous 'gutter traces'. Note car to right of image for scale. ; B – some of the wider iliophagous 'gutter traces' originally argued to be made by pliosaurs. Groove to the upper left is 3.5 metres long and attains a maximum width of 60cm, mark to the right of centre of view is 5.5 metres long and 45cm wide; C – broader view of bed, showing disposition of range of sizes of putative traces of benthic feeding (for scale, note figure, 1.8 metres high, in bottom left of photograph). All images courtesy of J. Geister.

to be an accumulation of *Pterodaustro* mandibles (fig. 11f). The sample had been retrieved during an annual student trip from a site some 300 km north of the Schultze excavation area (fig. 11g) (Martill *et al.*, 1999; Liston, 2004a). The block was recognised as a lump of *Leedsichthys* gill rakers, but with what appeared to be fenestrae along the length of the ramus (Martill *et al.*, 1999). These 'fenestrae' were used as the basis of erecting a new species of *Leedsichthys*, namely *Leedsichthys notocetes*, but subsequent analysis has revealed that these features actually appear to be erosional artefacts (Steel, pers. comm).

SUMMARY

It is interesting to contrast the perhaps understandable repeated confusion of the pachycormid *Leedsichthys* with a large acipenseroid fish (given the prominent gill rakers and branching finrays common to both) with the somewhat bizarre confusion between three utterly different bones of *Leedsichthys* and a stegosaurian dinosaur (other specimens of *Leedsichthys* have been misidentified as stegosaurian within the Sedgwick Museum's collections, but these have not been formally published). It emphasises the need for general awareness to be raised regarding the appearance and form of the remains of this remarkable animal.

CONCLUSIONS

An account has been given of the geographical and stratigraphical extent of *Leedsichthys*. Misidentifications have been addressed, with particular emphasis on the dorsal fin-rays and the hypobranchial element of the gill basket.

INSTITUTIONAL ABBREVIATIONS

PETMG = Peterborough Museum and Art Gallery, Cambridgeshire, England.

GLAHM = Hunterian Museum, The University of Glasgow, Scotland.

BMNH = Natural History Museum (London), England.

SMNK = Staatliche Museum für Naturkunde Karlsruhe, Germany.

I = Museo de Arqueologia, Antofagasta, Chile.

WMfN = Westphalisches Museum für Naturkunde, Münster, Germany.

PMM = Privatsammlung Matthias Metz, Bünde, Germany.

PHBW = Privatsammlung Harry Breitkreutz, Enger, Germany.

OUMNH = Oxford University Museum of Natural History, Oxfodshire, England.

JM SOS = Jura Museum, Eichstätt, Germany.


B


C

Figure 11- A – Map of Chile, showing Antofagasta and the 1994 and 1999 localities – S = Quebrada del Profeta, M = Quebrada Corral; B – I-190173 and C I8-021173, 2 specimens collected from east of Antofagasta Scale bar = 100mm.; D some of the material collected in 1978 by H.-P.Schultze Drawer is 500mm wide E - some of the material collected in 1994 by H.-P.Schultze Drawer is 500mm wide.; F – type specimen (SMNK 2573 PAL) of *Leedsichthys notocetes*; Scale bar = 100mm; G – type locality of *Leedsichthys notocetes* , with Frey (figure on left, 1.8m tall) for scale.

D

E

G

NMW = National Museums and Galleries of Wales, Cardiff, Wales.

LEICT = Museum and Art Gallery Leicester, Leicestershire, England.

CAMSM = Sedgwick Museum of Geology, University of Cambridge, England.

ACKNOWLEDGEMENTS:

Thanks to Ioannis Michelis for alerting me to the existence of the German specimen of *Leedsichthys*. Particular thanks to Ralf Metzdorf, Gudrun Humpohl, Rainer Ebel and Matthias Metz for their help and candour in straightening out the history of the German finds, the use of their photographs, their hospitality in Wallücke, and showing me their collected material from the Wiehen Mountains. To Lothar Schöllmann and Christina Reimann for enabling access to the material held in the Westfälisches Museum für Naturkunde, and to P. Martin Sander of the Goldfuss Museum in Bonn for access to histological samples of the Wallücke specimen.

To John Keen and Harry Breitkreutz , for access to material in their collection for study.

To Eric Buffetaut for introducing me to the French literary tradition, and arranging contacts with private collectors. To Gerard and Elizabeth Pennetier for their hospitality, and access to their beautiful collection of material from the length of the Villers-sur-Mer/Houlgate beach. To Jean-Luc Peart for providing hospitality and simultaneous translation in Paris, and Jean-Marie Guegan for facilitating access to material from Normandie beaches. Thanks to Joern Geister for photographs of the (now-landfilled) traces at Liesberg. Thanks to Mark Evans for pointing me in the direction of the almost unique Cap de la Hève material, and Dolf Gielen for photographs and images of this Kimmeridgian specimen of *Leedsichthys*.

Thanks to Leslie Noè, Colin Adams and Geoff Swinney for helpful discussion about benthic feeding. To Jon Jeffery, Anne Dulau, Jean-Luc Peart, Johannes Barth, Dino Frey and Kathrin Dietze for providing translations and hospitality.

Thanks to Dave Martill, Hans-Peter Schultze, Dino Frey and Gloria Arratia for giving me access to their specimens, photographs, field notes and recollections from excavations in the Atacama Desert in the seventies and nineties.

Thanks to Dave Martill and Dino Frey for comments on earlier drafts of this manuscript, to Alison Brown for support during European travel, to Sarah Earland for literature help, to Julian and Louis Leeds for access to their family's archives.

Special thanks and appreciation to Dave Martill for all his help and support over the years as Supervisor and to Colin Adams for his continuing role in this capacity.

REFERENCES

Anonymous 1921. Obituary. Henry Woodward. *Geological Magazine* LVIII: 481-484.

Arratia, G. 1996. The Jurassic and the early history of teleosts; pp 243-259. *In*: Arratia, G. & Viohl, G. (eds) *Mesozoic Fishes - Systematics and Paleoecology*. Verlag Dr. Friedrich Pfeil, Munchen.

Arratia, G. & Schultze, H-P. 1999. Mesozoic fishes from Chile; pp 565-593. *In*: Arratia, G. & Schultze, H-P. (eds) *Mesozoic Fishes 2 - Systematics and Fossil Record*. Verlag Dr. Friedrich Pfeil, München.

Bardet, N.; Pennetier, E.; Pennetier, G.; Charles, A. & Charles, J. 1993. Des os énigmatiques a section triangulaire dans le Jurassique Moyen (Callovien) de Normandie. *Bulletin Trimestriel de la Societé Géologique de Normandie et des Amis du Muséum du Havre*, 80: 7-10.

Blake, R.W. 1983. *Fish Locomotion*. Cambridge University Press, Cambridge, 205 pp.

Brown, D.S. 1990. Lincolnshire plesiosaur hunter discovers rich vertebrate fauna. *Geology Today*, 6(6): 182.

Brown, D.S. & Keen, J.A. 1991. An extensive marine vertebrate fauna from the Kellaways Sand (Callovian, Middle Jurassic) of Lincolnshire. *Mercian Geologist*, 12: 87-96.

Buffetaut, E. 1983. La paléontologie des vertébrés Mésozoïques en Normandie du 18e siècle à nos jours : Un essai historique. *Actes du Muséum de Rouen*, 1983: 39-59.

Delsate, D. 1999. *Haasichthys michelsi*, nov. gen., nov. sp., un nouveau Pachycormiforme (Osteichthyes, Actinopterygii) du Toarcien inferieur (Jurassique) luxembourgeois. *Travaux scientifiques Musée national d'Histoire naturelle de Luxembourg*, 1999: 87-140.

Dromart, G., Garcia, J-P., Gaumet, F., Picard, S., Rouseau, M., Atrops, F., Lécuyer, C. & Sheppard, S.M.F. 2003a. Perturbation of the Carbon Cycle at the Middle/Late Jurassic Transition: Geological and geochemical evidence. *American Journal of Science*, 303: 667-707.

Dromart, G., Garcia, J-P., Picard, S., Atrops, F., Lécuyer, C. & Sheppard, S.M.F. 2003b. Ice age at the Middle-Late Jurassic transition? *Earth and Planetary Science Letters*, 213: 205-220.

Flaubert, G. 1884. *Bouvard et Pécuchet*. Lemerre, Paris, 474 pp.

Gallois, R. 2005. Correlation of the Kimmeridgian succession of the Normandy coast, northern France with that of the Dorset-type area, southern England. *Comptes Rendus Geoscience*, 337: 347-355.

Galton, P.M. 1985. British plated dinosaurs (Ornithischia, Stegosauridae). *Journal of Vertebrate Paleontology*, 5: 211-254.

Geister, J. 1998. Lebesspuren von meersauriern und ihren beutetieren im Mittleren Jura (Callovien) von Liesberg, Schweiz. [Trace fossils made by marine reptiles and their prey in the Middle Jurassic (Callovian) of Liesberg, Switzerland.]. *Erlangen Facies*, 39: 105-124.

Grande, L. & Bemis, W.E. 1991. Society of Vertebrate Paleontology Memoir 1: Osteology and phylogenetic relationships of fossil and Recent paddlefishes (Polyodontidae) with comments on the interrelationships of Acipenseriformes. *Journal of Vertebrate Paleontology*, 11[1 - supplement], 121 pp. 1991.

Hans Nelson, C. & Johnson, K.R. 1987. Whales and walruses as tillers of the sea floor. *Scientific American*, 256: 74-81.

Hans Nelson, C., Johnson, K.R. & Barber Jr., J.H. 1987. Gray whale and walrus feeding excavation on the Bering Shelf, Alaska. *Journal of Sedimentary Petrology*, 57: 419-430.

Harland, W.B., Armstrong, R.L., Cox, A.V., Craig, L.E., Smith, A.G. & Smith, D.G. 1990. *A Geologic Time Scale*. Cambridge University Press, Cambridge, 263 pp.

Hauff, B. 1953. *Ohmdenia multidentata* nov. gen. et nov. sp. Ein neuer großer Fischfund aus den Posidonienschiefern des Lias & von Ohmden/Holzmaden in Württemberg. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 97: 39-50.

Hauff, B. & Hauff, R.B. 1981. *Das Holzmadenbuch*. REPRO-DRUCK GmbH, Fellbach, 138 pp.

Hoffstetter, R. 1957. Quelques observations sur les Stégosaurinés. *Bulletin du Muséum National d'Histoire Naturelle Paris*, 29: 537-547.

Huene, F.v. 1901. Notizen aus dem Woodwardian-Museum in Cambridge. *Centralblatt für Mineralogie, Geologie und Paläontologie*, 1901: 715-719.

Hulke, J.W. 1887. Note on some Dinosaurian remains in the collection of A. Leeds Esq., of Eyebury, Northamptonshire. *Quarterly Journal of the Geological Society of London*, 43: 695-702.

Jobling, M. 1995. *Environmental Biology of Fishes*. Chapman & Hall Fish and Fisheries Series, 16. Chapman & Hall, London, 449 pp.

Knight, W.C. 1898. Some new Jurassic vertebrates from Wyoming. *American Journal of Science*, CLV: 378-381.

Lambers, P. 1992. *On the Ichthyofauna of the Solnhofen Lithographic Limestone (Upper Jurassic, Germany)*. Rijksuniversiteit Groningen, 336 pp.

Leeds, A.N. 1901. Letter from Alfred Nicholson Leeds to Arthur Smith Woodward (22/12/1901).

Leeds, E.T. 1956. *The Leeds Collection of Fossil Reptiles*. Oxford, 104 pp.

Leeds, A.N. & Smith Woodward, A. 1897. Report on a Field-trip to Peterborough. *Proceedings of the Geological Association*, 15: 190-192.

Liston, J.J. 2004a. An overview of the pachycormiform *Leedsichthys*; pp 379-390. *In*: Arratia, G. & Tintori, A. (eds) *Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity*. Verlag Dr. Friedrich Pfeil, München.

Liston, J.J. 2006. From Glasgow to the Star Pit and Stuttgart: A short journey around the world's longest fish. *The Glasgow Naturalist*, 24, part 4: 59-71.

Liston, J. J. 2007. A Fish Fit For Ozymandias?: The Ecology, Growth and Osteology of Leedsichthys (Pachycormidae, Actinopterygii). Unpublished PhD Thesis. 464 pages. Faculty of BioMedical & Life Sciences, University of Glasgow, Scotland.

Liston, J. J. 2008. *Leedsichthys* des Vaches Noires au peigne fin (translation by M-C Buchy) *L'Écho des Falaises*, 12: 41-49.

Liston, J.J. & Noè, L.F. 2004. The tail of the Jurassic fish *Leedsichthys problematicus* (Osteichthyes: Actinopterygii) collected by Alfred Nicholson Leeds - an example of the importance of historical records in palaeontology. *Archives of Natural History*, 31: 236-252.

Marsh, O.C. 1880. Principal characters of American Jurassic Dinosaurs. Part III. *American Journal of Science*, XIX: 253-259.

Marsh, O.C. 1881. Principal characters of American Jurassic Dinosaurs. Part IV. Spinal cord, pelvis and limbs of *Stegosaurus*. *American Journal of Science*, XXI: 167-170.

Marsh, O.C. 1887. Principal characters of American Jurassic Dinosaurs. Part IX. The skull and dermal armor of *Stegosaurus*. *American Journal of Science*, XXXIV: 413-417.

Marsh, O.C. 1889. Comparison of the principal forms of the Dinosauria of Europe and America. *American Journal of Science*, XXXVII: 323-336.

Martill, D.M. 1991. Chapter 9 Fish. pp.197-225. *In*: Martill, D.M. & Hudson, J.D. (eds) *Fossils of the Oxford Clay*. Henry Ling Ltd., Dorchester.

Martill, D.M., Frey, E., Caceras, R.P. & Diaz, G.C. 1999. The giant pachycormid *Leedsichthys* (Actinopterygii) in the southern hemisphere: further evidence for a Jurassic Atlanto-Pacific marine faunal province. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1999: 243-256.

McAllister, D.E. 1968. Evolution of branchiostegals and classification of teleostome fishes. *National Museum of Canada Bulletin*, 221: 1-229.

Michelis, I., Martin Sander, P., Metzdorf, R. & Breitkreuz, H. 1996. Die vertebratenfauna des Calloviums (Mittlerer Jura) aus dem Steinbruch Störmer (Wallücke, Wiehengebirge). [The Callovian (Middle Jurassic) vertebrate fauna of the Störmer Quarry (Wallücke, Wiehengebirge).]. *Geologie und Paläontologie in Westfalen*, 44: 5-66.

Murray, J.M.H., Meadows, A. & Meadows, P.S. 2002. Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. *Geomorphology*, 47: 15-30.

Neaverson, E. 1935. Reptiles from the Oxford Clay of Peterborough in the geological collection of the University of Liverpool. *Proceedings of the Liverpool Geological Society*, 67th Session 16: 234-262.

Noè, L.F. 2001. *A taxonomic and functional study of the Callovian (Middle Jurassic) Pliosauroidea (Reptilia, Sauropterygia).* Volume 1 - text. University of Derby, 347 pp.

Noè, L.F.; Liston, J.J. & Evans, M. 2003. The first relatively complete exoccipital-opisthotic from the braincase of the Callovian pliosaur, *Liopleurodon*. *Geological Magazine*, 140: 479-486.

Porter, H. 1861. The Oxford Clay. *The Geology of Peterborough and its Vicinity*. T. Chadwell, Peterborough, pp 61-87.

Probst, E. & Windolf, R. 1993. *Dinosaurier in Deutschland*. Bertelsmann, München, 320 pp.

Radwańska, U. 2004. Tube-dwelling polychaetes from the Upper Oxfordian of Wapienno/Bielawy, Couiavia region, north-central Poland. *Acta Geologica Polonica*, 54: 35-52.

Riccardi, A.C. 1991. Jurassic and Cretaceous marine connections between the Southeast Pacific and Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 87: 155-189.

Smith Woodward, A. 1889a. Preliminary notes on some new and little-known British Jurassic fishes. *Geological Magazine*, Decade 3 Volume 6: 448-455.

Smith Woodward, A. 1889b. On the palaeontology of sturgeons. *Proceedings of the Geological Association*, 11: 24-44.

Smith Woodward, A. 1895. Family Pachycormidae; pp 374-414. *In*: *Catalogue of the Fossil Fishes in the British Museum (Natural History)*, Volume 3. British Museum (Natural History), London.

Smith Woodward, A. 1916. On a new specimen of the Liassic pachycormid fish *Saurostomus esocinus*, Agassiz. *Geological Magazine*, Decade VI Volume 3: 49-51.

Sokolov, L.I. & Vasil'ev, V.P. 1989. *Acipenser baeri* Brandt, 1869; pp 263-284. *In*: Holcik J (ed.) *Vol. 1, Part II General Introduction to Fishes Acipenseriformes*. AULA-Verlag GmbH, Wiesbaden.

Townsend, A.C. 1962. A. S. Woodward's first day at the British Museum (Natural History), 24 August 1882. *Journal of the Society for the Bibliography of Natural History*, 4: 79-83.

Uhlir, D.M., Akers, A. & Vondra, C.F. 1988. Tidal inlet sequence, Sundance Formation (Upper Jurassic), north-central Wyoming. *Sedimentology*, 35: 739-752.

Van Den Berg, C., Sibbing, F.A., Osse, J.W.M. & Hoogenboetem, W. 1992. Structure, development and function of the branchial sieve of the common bream, *Abramis brama*, white bream, *Blicca bjoerkna*,and roach, *Rutilus rutilus*. *Environmental Biology of Fishes*, 33: 105-124.

Van Den Berg, C., Van Den Boogaart, J.G.M., Sibbing, F.A. & Osse, J.W.M. 1994. Implications of gill arch movements for filter-feeding: an X-ray cinematographical study of filter-feeding white bream (*Blicca bjoerkna*) and common bream (*Abramis brama*). *Journal of Experimental Biology* 191: 257-282.

Weems, R.E. & Blodgett, R.B. 1996. Geologic Studies in Alaska by the U.S. Geological Survey, 1994. The pliosaurid *Megalneusaurus*: a newly recognized occurrence in the Upper Jurassic Naknek Formation of the Alaskan Peninsula. 1996. *U.S. Geological Survey Bulletin*, 2152: 169-176.

Wenz, S. 1967. Compléments à l'étude des poissons actinoptérygiens du Jurassique Français. *Cahiers de Paléontologie*. 276 pp.

Whatley, R. & Ballent, S. 1994. Bi-hemispherical distribution of Jurassic Ostracoda: Palaeogeographical implications. *Centralblatt für Mineralogie, Geologie und Paläontologie*: 961-966.

Woodward, H. 1899. Othniel Charles Marsh, LL. D. (Yale), Ph. D. (Heidelberg). *Geological Magazine* Decade IV Volume 6 (=volume 36): 237-240.

Zittel, K.A.v. 1925. *Text-Book of Palaeontology*. In: Eastman, C.R. & Smith Woodward, A. (eds) Macmillan and Co., Limited, London. 283 pp.

Annexes

Table 1. Details of the most relevant specimens of *Leedsichthys* mentioned in the text

Specimen number	Collector/collection	Date Collected	Locality	Description
GLAHM 132787	D. Gielen/Hunterian Museum	2004	Cap de la Hève, Normandie	single gill raker plus many lepidotrichia
private	G. & E. Pennettier	1980s-1990s	Vaches Noire, Normandie	gill rakers plus ceratobranchial elements
BMNH 32581	Tesson of Caen	1857	Vaches Noire, Normandie	cluster of disarticulated gill rakers
WMfN PM 17006/8	Westfalisches Museum	July 1982-November 1983	Wallücke	hypobranchial
WMfN PM 17006/1	Westfalisches Museum	July 1982-November 1983	Wallücke	(?caudal) fin-rays with possible traces of tendons
WMfN PM 17005/2	Westfalisches Museum	July 1982-November 1983	Wallücke	distal extremities of 2 ?dorsal fin-rays
WMfN PM 17005/23	Westfalisches Museum	July 1982-November 1983	Wallücke	piece with texture like crest of hyomandibula or edge of parietal
WMfN PM 17005/24	Westfalisches Museum	July 1982-November 1983	Wallücke	possible opercular series of plates
PHB W 138/4	Breitkreutz	July 1982-November 1983	Wallücke	?left cleithral fragment
PMM 19.1-21.1, 23.1	Metz	July 1982-November 1983	Wallücke	?supraangular
GLAHM 109518	Hunterian Museum	Jul-02	Wallücke	isolated ray fragments
BMNH P.6921	Alfred N. Leeds	pre-1887	Peterborough district	holotype specimen: dorsal, pectoral and caudal fin-rays, skull etc.
BMNH P.6922	Alfred N. Leeds	pre-1887	Peterborough district	preopercle plus two fragments
BMNH P.10000	Alfred N. Leeds	March 1898	Peterborough district	skull material with gill rakers, cleithra, parasphenoid and tail
BMNH P.10156	Alfred N. Leeds	Jul-05	Peterborough district	articulated gill basket with left hyomandibula, ?supraangular
BMNH P.66340	Alfred N. Leeds	pre-1919	Peterborough district	primarily jaw elements, including right dentary, ?supraangular
BMNH 46355	William Cunnington	1875	Christian Malford, Wiltshire	isolated ray fragment
PETMG F.174	Peterborough Museum	2001-2003	Whittlesey, Peterborough	skull, fin and gill raker material
CAMSM J.46873	Henry Keeping	1898	Fletton, Peterborough	dorsal fin-rays
SMNK 2573.PAL	Karlsruhe Museum	1998	Quebrada Corral, Chile	disarticulated gill rakers
I-190173	Museo de Arqueologia, Antofagasta	Jan-73	east of Antofagasta	disarticulated gill rakers
I8-021173	Museo de Arqueologia, Antofagasta	Nov-73	east of Antofagasta	articulated series of gill rakers
(unnumbered)	Museo Nacional de Historia Natural, Santiago	1994	Quebrada del Profeta, Chile	gill rakers plus unprepared material

Table 2a. Details of *Leedsichthys* specimens in Sedgwick Museum collections.

Accession no.	Collector	Date	Locality	Description
CAMSM J.27416	[unknown]	1899	Fletton [Huntingdonshire]	hypobranchial
CAMSM J.27417	[unknown]	1899	Fletton [Huntingdonshire]	?hypobranchial
CAMSM J.27418	[unknown]	1899	Fletton [Huntingdonshire]	partial callus formation
CAMSM J.27419	[unknown]	1899	Fletton [Huntingdonshire]	partial callus formation
CAMSM J.27420		1901	Fletton [Huntingdonshire]	preopercular ridge fragment
CAMSM J.27421		1901	Fletton [Huntingdonshire]	possible dorsal fin spine tip
CAMSM J.27422		1901	Fletton [Huntingdonshire]	possible dorsal fin spine tip
CAMSM J.27423		1901	Fletton [Huntingdonshire]	possible dorsal fin spine tip
CAMSM J.27424				PLIOSAUR EXOCCIPITAL-OPISTHOTIC
CAMSM J.27425	?	?	Whittlesea	odd ‘junction’ bone - tip of a lepidotrichium? Like J.67424
CAMSM J.27426	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment
CAMSM J.27427	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment
CAMSM J.27428	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragmentt - links to J.27433
CAMSM J.27429	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment
CAMSM J.27430	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment
CAMSM J.27431	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment (2)
CAMSM J.27432	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment
CAMSM J.27433	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment - links to J.27428
CAMSM J.27434	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	?juvenile hypobranchial?
CAMSM J.27435	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	unident. frag. (1)
CAMSM J.27436	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	unident. frag. (1)
CAMSM J.27437	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	possible propercular fragment (1)
CAMSM J.27438	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	hypobranchial (1)
CAMSM J.27439	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	proximal radial (1)
CAMSM J.27440	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	dorsal fin spine (1)
CAMSM J.27441	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	proximal radial (1)
CAMSM J.27442	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	proximal radial (1)
CAMSM J.27443	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	dorsal fin spine (1)
CAMSM J.27444	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	dorsal fin spine or curved element, possible tooth mark
CAMSM J.27445	Alfred Nicholson Leeds	?	[Fletton, Northamptonshire]	bifurcating fin ray (4)
CAMSM J.35320	?	?	[Fletton, Northamptonshire]	connects to X.50124/LP.15 - left parietal with ceratobranchial and mass of gill rakers (“showing hooks on ‘branchiostegal’”)
CAMSM J.46873	Henry Keeping	1899	[Fletton, Northamptonshire]	dorsal fin ray series (figured by von Huene) including dorsal ‘support’?, a-right hyomandibula

Accession no.	Collector	Date	Locality	Description
CAMSM J.46874	Henry Keeping	1898	[Fletton, Northamptonshire]	stegosaur armour (figured by HG Seeley)
CAMSM J.46875				UNSEEN
CAMSM J.46876		1899	Fletton [Huntingdonshire]	dorsal fin spine
CAMSM J.46877		1902	Whittlesea	dorsal fin spine
CAMSM J.46878		1902	Whittlesea	dorsal fin spine
CAMSM J.46879	Henry Keeping	1902	Whittlesea	stegosaur tail spine
CAMSM J.66124			Whittlesea	J.66124/6/7/8 all join to make root of caudal ray like V3362 (“plesiosaurian”)
CAMSM J.66126			Whittlesea	J.66124/6/7/8 all join to make root of caudal ray like V3362 (“?crocodilian”)
CAMSM J.66127			Whittlesea	J.66124/6/7/8 all join to make root of caudal ray like V3362 (“?crocodilian”)
CAMSM J.66128			Whittlesea	J.66124/6/7/8 all join to make root of caudal ray like V3362 (“?crocodilian”)
CAMSM J.66920	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	pectoral fragment
CAMSM J.66921	?	1899	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66922	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	pectoral fragment
CAMSM J.66923	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	distal end of preopercle
CAMSM J.66924	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66925	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66926	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66927	?	?	?	parts of two adjacent ceratobranchials
CAMSM J.66928	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	two hypobranchials
CAMSM J.66929	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	pectoral fragment
CAMSM J.66930	Henry Keeping (‘H.K.’)	1900	[Fletton, Northamptonshire]	two hypobranchials
CAMSM J.66931	?	1900	[Fletton, Northamptonshire]	mass of gill rakers
CAMSM J.66932	?	1900	[Fletton, Northamptonshire]	mass of gill rakers
CAMSM J.66933	Henry Keeping (‘H.K.’)	1900	[Fletton, Northamptonshire]	ceratobranchial fragment
CAMSM J.66935	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66936	?	1899	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66937	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66938	?	1898d	Fletton [Huntingdonshire]	bone fragments - ?left preopercle, 593mm long
CAMSM J.66939	?	?	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66940	Henry Keeping (‘H.K.’)	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66941	?	?	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66942	?	?	[Fletton, Northamptonshire]	J.66942 glued to J.66943 - ceratobranchial termination
CAMSM J.66943	?	?	[Fletton, Northamptonshire]	J.66942 glued to J.66943 - ceratobranchial termination
CAMSM J.66944	?	?	[Fletton, Northamptonshire]	tip of probable caudal fragment
CAMSM J.67413	?	1898d	Fletton [Huntingdonshire]	unident. frag. (resemblance to ophthalmosaur prefrontal/postorbital)

Accession no.	Collector	Date	Locality	Description
CAMSM J.67414	?	1898d	Fletton [Huntingdonshire]	proximal end of dorsal fin spine
CAMSM J.67415	?	1898d	Fletton [Huntingdonshire]	radiale fragment
CAMSM J.67416	?	1898d	Fletton [Huntingdonshire]	strongly curved element (like eg V3363, but much smaller) although passing resemblance to ophthalmosaur left clavicle
CAMSM J.67417	?	1898d	Fletton [Huntingdonshire]	small ‘starred’ bone like Cambridge V.787
CAMSM J.67418	?	1898d	Fletton [Huntingdonshire]	radiale fragment
CAMSM J.67419	?	1898d	Fletton [Huntingdonshire]	large circular articular surface - unident. - resembles ‘joint’ of Butterfly bone
CAMSM J.67420	?	1898d	Fletton [Huntingdonshire]	bone fragments - right parietal (juvenile)
CAMSM J.67421	?	1898d	Fletton [Huntingdonshire]	distal part of preopercle or Butterfly bone
CAMSM J.67422	?	1898d	Fletton [Huntingdonshire]	strong resemblance to GLAHM ?gastralium (possibly pathological - NOT V1688)
CAMSM J.67423	?	1898d	Fletton [Huntingdonshire]	dorsal fin spine element, possibly with flattened callus/joint
CAMSM J.67424	?	1898d	Fletton [Huntingdonshire]	circular articular surface, like J.27425, possible teeth fragments embedded in it
CAMSM J.67425	?	1898d	Fletton [Huntingdonshire]	proximal radial fragment
CAMSM J.67426	?	1898d	Fletton [Huntingdonshire]	distal end of dorsal fin spine
CAMSM J.67427	?	1898d	Fletton [Huntingdonshire]	possible dorsal fin spine, but severely damaged
CAMSM J.67428	?	1898d	Fletton [Huntingdonshire]	possible dorsal fin spine, but severely damaged
CAMSM J.67429	?	1898d	Fletton [Huntingdonshire]	character of pectoral fin, possibly near base
CAMSM J.67430	?	?	[Fletton, Northamptonshire]	as J.67423
CAMSM J.67431	?	?	[Fletton, Northamptonshire]	?hypobranchial
CAMSM J.67432	?	1898d	Fletton [Huntingdonshire]	as J.67423
CAMSM J.67433	?	?	[Fletton, Northamptonshire]	base of dorsal fin spine
CAMSM J.67434	?	?	[Fletton, Northamptonshire]	distal fragment of anal fin support
CAMSM J.67435	?	?	[Fletton, Northamptonshire]	as J.27425
CAMSM J.67436	?	?	[Fletton, Northamptonshire]	possible pectoral-related element
CAMSM J.67437	?	1898d	Fletton [Huntingdonshire]	inferior end of left cleithrum (see F.174/10,004)
CAMSM J.67438	?	1898d	Fletton [Huntingdonshire]	possible distal end of left parietal (see J.67420 and P.6921)
CAMSM J.67439	?	1898d	Fletton [Huntingdonshire]	unident. frag.
CAMSM J.67440	?	1898d	Fletton [Huntingdonshire]	elongate element, possibly dorsal fin spine
CAMSM J.67441	?	?	[Fletton, Northamptonshire]	striated caudal ray
CAMSM J.67442	?	?	[Fletton, Northamptonshire]	striated and bifurcating caudal ray with possible breaks callus/joints
CAMSM J.67443	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67444	?	?	[Fletton, Northamptonshire]	striated caudal ray (possibly bifurcating) with possible break callus/joint
CAMSM J.67445	?	?	[Fletton, Northamptonshire]	striated caudal ray bifurcating with possible break callus/joint
CAMSM J.67446	?	?	[Fletton, Northamptonshire]	striated caudal ray, possibly broken through callus
CAMSM J.67447	?	?	[Fletton, Northamptonshire]	striated caudal ray, possibly broken through callus
CAMSM J.67448	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67449	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end

Accession no.	Collector	Date	Locality	Description
CAMSM J.67450	?	?	[Fletton, Northamptonshire]	distal tail ray fragment (just after bifurcation point)
CAMSM J.67451	?	?	[Fletton, Northamptonshire]	bifurcating distal caudal ray, one hemitrichium missing (segment?)
CAMSM J.67452	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67453	?	?	[Fletton, Northamptonshire]	possible hypobranchial
CAMSM J.67454	?	?	[Fletton, Northamptonshire]	caudal ray fragment with callus growth
CAMSM J.67455	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67456	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67457	?	?	[Fletton, Northamptonshire]	striated caudal ray, possibly broken through callus
CAMSM J.67458	?	?	[Fletton, Northamptonshire]	striated caudal ray, possibly broken through callus
CAMSM J.67459	?	?	[Fletton, Northamptonshire]	caudal ray fragment
CAMSM J.67460	?	?	[Fletton, Northamptonshire]	segment/callus in tail ray
CAMSM J.67461	?	?	[Fletton, Northamptonshire]	stump of lepidotrichium (cast prior to growth ring sectioning by TJC)
CAMSM J.67462	?	?	[Fletton, Northamptonshire]	segment/callus in tail ray
CAMSM J.67463	?	?	[Fletton, Northamptonshire]	segment/callus in tail ray
CAMSM J.67464	?	?	[Fletton, Northamptonshire]	possible hypobranchial
CAMSM J.67465	?	?	[Fletton, Northamptonshire]	caudal ray fragment
CAMSM J.67466	?	?	[Fletton, Northamptonshire]	segment/callus in tail ray, at bifurcation
CAMSM J.67467				gill raker
CAMSM J.67468				segment/callus in tail ray
CAMSM J.67469				segment/callus in tail ray, at bifurcation
CAMSM J.67470				striated caudal ray with flattened end
CAMSM J.67471	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	hypobranchial (1)
CAMSM J.67472	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67479
CAMSM J.67473	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67477
CAMSM J.67474	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	right cleithrum (1), ALMOST connects to J.67478
CAMSM J.67475	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	?left cleithrum (1)
CAMSM J.67476	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67480
CAMSM J.67477	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67473
CAMSM J.67478	Henry Keeping ('H.K.')			right cleithrum (1), ALMOST connects to J.67478
CAMSM J.67479	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67472
CAMSM J.67480	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67476
CAMSM J.67481		1897	Fletton [Huntingdonshire]	anal fin support
CAMSM J.67483	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	pectoral fragment
CAMSM V.787				mid-line structure, see LEICT G.1105.1899

Accession no.	Collector	Date	Locality	Description
CAMSM X.39250				SWEEPINGS' TAIL SPECIMEN - probable caudal, the proximal part of X.50125, combined length of just over 1.3 metres
CAMSM X.50109	?	1898d	Fletton [Huntingdonshire]	LP6 - left preopercular ridge (with articular points/callus growth?)
CAMSM X.50110	?	1898d	Fletton [Huntingdonshire]	LP5 - dorsal fin spine (see LEICT G.474.1897 and G.475.1897) with anterior/ posterior flexion
CAMSM X.50111	?	1898d	Fletton [Huntingdonshire]	LP8 - dorsal fin spine
CAMSM X.50112	?	1898d	Fletton [Huntingdonshire]	LP16 - right cleithrum
CAMSM X.50113	?	1899	Fletton [Huntingdonshire]	LP1 - right preopercular ridge
CAMSM X.50114	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	LP4 - right ceratohyal
CAMSM X.50115	?	1901	Fletton [Huntingdonshire]	LP2 - hypobranchial
CAMSM X.50116	?	1901	Fletton [Huntingdonshire]	LP7 - (see 'yellow' identical bone in G.128.1900) - same labels as J.27420-J.27423 (see also unnumbered Ox. Clay Fletton 1901 pyrite crisis with NO LP or other number)
CAMSM X.50117	?	1902	Whittlesea	LP9 - ?label like 46877 and 46878 - dorsal fin spine
CAMSM X.50118	?	?	Whittlesea	LP3 - hypobranchial
CAMSM X.50119	?	?	?	LP10 - branchial arch fragment
CAMSM X.50120	?	?	?	LP11 - piece of ceratobranchial with mass of gill rakers (reminiscent of J.35320/ LP.15)
CAMSM X.50121	?	?	?	LP12 - X.50121-X.50123 form two parallel ceratobranchials
CAMSM X.50122	?	?	?	LP13 - X.50121-X.50123 form two parallel ceratobranchials
CAMSM X.50123	?	?	?	LP14 - X.50121-X.50123 form two parallel ceratobranchials
CAMSM X.50124	?	?	?	LP15 - ceratobranchial fragment with mass of gill rakers - connects to J.35320
CAMSM X.50125	?	?	?	LP17 - distal part of probable caudal X.39250 (combined length of 1.3 metres)

Table 2b. Details of *Leedsichthys* specimens in New Walk and Leicester University Museum collections.

Accession no.	Collector	Date	Locality	Description
LEICT G1102.1899	Swales R Mr (gift)			Board of pectoral fin ray fragments
LEICT G1103.1899	Swales R Mr (gift)			Board of mounted gill rakers
LEICT G1104.1899	Swales R Mr (gift)			unident. bone - apparently connects to G.1105.1899 (see also two examples in P.6930 and one in V3363)
LEICT G1105.1899	Swales R Mr (gift)			unident. bone - apparently connects to G.1104.1899 (see also two examples in P.6930 and one in V3363)
LEICT G1106.1899	Swales R Mr (gift)			(from board, this could G1.2005 - else unseen)
LEICT G1107.1899	Swales R Mr (gift)			six bones: proximal end of L dentary, inferior end of L cleithrum, superior end of L cleithrum, end of ceratobranchial (like P.11823), plus two other bones only represented in V3363
LEICT G128.1900	Swales R Mr (gift)			left parietal, ?symplectic, basiocciput, left and right preopercular ridges, 4 ceratobranchials with pectoral fin raysand gill rakers showing fine structure, one piece like J.67421, one piece like LP.7/X.50116
LEICT G236.1902 / G520.1993	Swales R Mr (gift)		Oxford Clay of Peterborough	(B5, =G.520.1993) two fin ray/lepidotrichial elementsmost resemble pectoral rays, although slightly smoother than might be expected
LEICT G418.1956.15	Peterborough Museum Society (purchase) originally PJ Phillips	1919	Fletton	three bones: 1374= .5=left hypobranchial, .2=right hypobranchial, .4=end of ceratobranchial (.1 and .3 unseen)
LEICT G471.1897	Swales R Mr (gift)/ Pocock	15/7/1896	Oxford Clay of Peterborough	dorsal fin spine - resembles a proximal radial (although groove poorly defined on one side)
LEICT G472.1897	Swales R Mr (gift)/ Pocock	15/7/1896	Oxford Clay of Peterborough	dorsal fin spine
LEICT G473.1897	Swales R Mr (gift)/ Pocock	15/7/1896	Oxford Clay of Peterborough	dorsal fin spine
LEICT G474.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	(B6) dorsal fin spine, with anterior/posterior flexion
LEICT G475.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	(B6) dorsal fin spine
LEICT G476.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G477.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G478.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G479.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G765.1898	Swales R Mr (gift)			R hyomandibula
LEICT G343.1896	Swales R Mr (gift)		Oxford Clay of Peterborough	(B2) dorsal fin spine, ‘clavicular’ form
LEICT G344.1896	Swales R Mr (gift)		Oxford Clay of Peterborough	(B2) dorsal fin spine, see V3363 for one
LEICT G345.1896	Swales R Mr (gift)		Oxford Clay of Peterborough	(B2) dorsal fin spine

Accession no.	Collector	Date	Locality	Description
LEICT G451.1992	Swales R Mr (gift)			.1-.7=(former 02/107 or 107Xw'02) - unseen, but probably pectoral fin-rays
LEICT G519.1993	Swales R Mr (gift)	1902	Oxford Clay of Peterborough	.1-.7=dorsal fin spines (former 02/235 or 235Xw'02 "ichthyosaur ribs") - unseen
LEICT G1312.1899	purchase unknown		Oxford Clay of Peterborough	(B1) four proximal radials and two dorsal fin spines (including one possible anterior/posterior flexion).
LEICT G393.1896	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G3348.1898	purchase unknown		Oxford Clay of Peterborough	unseen
LEICT G1.2005				parasphenoid (could be G.1106.1899)
LEICT G1.2010.1	Nick Oliver	1998	Kempston Quarry	3D preserved ceratobranchials on underside of dermatocranium
LEICT G1.2010.2	Nick Oliver	1997	Dogsthorpe Pit landfill	Overlying dermatocranial elements
LEIUG 96085	David Michael Martill	1987	Dogsthorpe Pit	gill raker
LEIUG 96086	David Michael Martill	1979	[Market Deeping]	fragments of actinotrichia, gill-rakers, fin-rays, ceratobranchials
LEIUG 96087	P.C. Schultz	1973	[Orton Pit]	ceratobranchial, pectoral fin-ray and gill raker fragments - /24 has special gill raker feature
LEIUG 114604	Martill & Hollingworth	1991	LBC pit, Calvert	concretion with pectoral fin-rays and two radiales, also associated pectoral fin-ray, preopercular and cleithral fragments

Table 2c. Details of Leedsichthys specimens in Oxford University and Peterborough Museum collections.

Accession no.	**Collector**	**Date**	**Locality**	**Description**
OUMNH J.1803	ET Leeds, Woodstock Road		dorsal fin spine - was on wall of his house until 1950 - as collected by his dad.	
OUMNH J.1803/1	A.M. Bell, Balliol College	1894	OC of Wolvercote, NW of Oxford	Lived in north Oxfordshire and donated occasional pieces.dorsal fin spine
PETMG F1				hyomandibula, dorsal fin spine, hypobranchial - other unaudited material at PETMG
PETMG F2	John Phillips			1425 - hypobranchial - other unaudited material at PETMG
PETMG F34	John Phillips		King's Dyke	1466 - partial skull with damaged remains of skull roof, branchial basket and jaws
PETMG F121	David Michael Martill	1984	Buntings Lane, near Farcet	lepidotrichial fragments, including pectoral fin rays
PETMG F124				with F.121 - lepidotrichial fragments
PETMG F174	Liston/Dawn/Martill et al.	2001-2003	Star Pit, Whittlesey	ARISTON - UNDER PREP. - paired pectoral fins (/10025, /10002), preopercles and hyomandibulae; fused parietals and paired dermopterotics; /2052 gill raker figured, /10004 right cleithrum, /182 left preopercle, /245 radiale I, /263 radiale II, /264 lpdt, dorsal fin spines, hypobranchial, ceratobranchial III, actinotrichia, ceratohyal, many gill rakers
PETMG R189				dorsal fin spine, hypobranchial - extracted from Muraenosaurus leedsi specimen.

Table 2d. Details of *Leedsichthys* specimens in Hunterian Museum Collection, University of Glasgow.

Accession no..	**Collector/number of parts**	**Date**	**Locality**	**Description**
GLAHM V3362	1			branching caudal fin ray (1225mm long)
GLAHM V3363	904			12 numbered and paired from January 1915 sale, left maxilla, left ceratohyal, left ?preopercle, left preopercular ridge, 'ribs', anal fin supports (5), proximal radials (8), right parietal, 5 hypobranchials, 4 ceratobranchials (parts 6 & 7), ?4 epibranchials (parts 9 & 10), dorsal fin spines (63), 2-way branching fused supraneural, robust curved elements (6), cleithral fragment (part 8 - former 'dentary'), 2 ?hyomandibulae (parts 1 & 5), caudal fin ray fragments, 2 gill-rakers, callus broken bone, unidentified dermatocranial elements (paired 12 & 4), 11 unidentified bone, butterfly' bone (pathological cleithum?), basiocciput
GLAHM 109518 & GLAHM 109519	JJ Liston	July 2002	Stormer Quarry, Wallücke.	Fragments/gill fragments.

GLAHM 132787	Dolf Gielen	2004	Cap de la Heve, Normandie.	Gill raker and several fin rays.

Table 1e. Details of *Leedsichthys* specimens, collected by Alfred Nicholson Leeds in Natural History Museum (London) collections.

Specimen number	**Number of parts**	**Description (as given in BMNH accession and purchase registers)**	**Description**
BMNH P.6921	1,133	"Associated series of bones, the type specimen..."***//"Bones of Leedsia 180 specimens" [part of batch]	gill rakers (89), ceratobranchials (2 x first), epibranchials (2 x second plus 1 indet.), lepidotrichia, parietals, left cleithrum, cleithrum-like element, hypobranchials (4, 2 red), hypobranchial-like mass, distal actinotrichia (4), radiale II, radiale I, thin unknown, left ceratohyal, partial right ceratohyal, ?branched supraneural, ?bromalite/coprolite, associated Pachymylus tooth plate, 17 lengths of dfs (of which 10 red-marked), 1c-b + pec (mainly unprepared from the clay) + caudal fin-rays, 2 bones with callus breaks
BMNH P.6922	8	""Preoperculum or clavicle", doubtfully associated with above, described ibid. p.453, no.6."//[as P.6921]	right preopercle with 2 fragments
BMNH P.6923	27	"A pair of large flat bones, and two supposed "branchial arches". (4)"//[as P.6921]	2 ceratobranchials with 2 unidentified cranial elements
BMNH P.6924	19	"Series of supposed "branchiostegal rays", found associated. (10)"[as P.6921]	dorsal fin spines (7)
BMNH P.6925	243	"Miscellaneous "branchiostegal rays", one noticed loc. cit. p.453 (25)"[as P.6921]	dorsal fin spines (30 plus frags- includes robust curved element from type description - possibly some from P6924, noting callus), proximal radials (11 plus frags), caudal fin ray fragments (11), left preopercular ramus, cleithral fragments, ?ceratohyal fragment, left ?maxillary fragment
BMNH P.6926	199	"Two associated portions of supposed branchial arches. (2)"[as P.6921]	2 ceratobranchials with pectoral fin ray fragments
BMNH P.6927	37	"Two associated undetermined bones. (2)"[as P.6921]	cleithrum-like fragment, right ?preopercle-like bone (compare with Fig. 8.35 top) 575mm long plus 2 other preopercle-like fragments (probably from other specimens)
BMNH P.6928	35	"Associated series of bones. (12)"[as P.6921]	proximal radial fragment, ceratobranchial, left ceratohyal, right anal fin support, dorsal fin spine fragment, 9 'tips' plus V787-like bone
BMNH P.6929	83	"Associated fin-rays."//[as P.6921]	pectoral fin ray fragments
BMNH P.6930	352	"Miscellaneous bones."//[as P.6921]	epibranchial (1), left supramaxilla, both nasals, caudal fin rays, paired cleithrum-like frags-undeveloped???, ceratohyal (left), ceratobranchials (3), possible paired entopterygoids?, ridged dermatocranial element (postparietal?), roughened dermatocranial elements, possible dermopterotic, fragments of parasphenoid, ?small parietal?
BMNH P.8609	5	" - (1)"//"unnamed fish plates and bones"	right cleithrum with ?ceratobranchial fragment and two lepidotrichial fragments (one with ?callus)
BMNH P.8610	17	"gill-rakers. (12)"//"unnamed fish plates and bones"	gill rakers (17)

Specimen number	Number of parts	Description (as given in BMNH accession and purchase registers)	Description
BMNH P.10000	many	“Tail + associated bones (1)”//”A set of fish remains of Leedsia problematica”	both caudal lobes, ?left pectoral fin fragment, pyritised ceratohyal, left hyomandibula, both cleithra, both epibranchial Is, 3 ceratobranchial fragments, parasphenoid, 2 ‘preopercle-esque’ bones, gill rakers (possibly one with ‘mesh’), lepidotrichial fragments, 3 ?pliosaur epipodials are associated with this specimen
BMNH P.10156	many	“Hyom. + br. arches. (1)”//”Leedsia problematica, hyomandibular + branchial arches”	gill basket, left hyomandibula, ?pectoral fin rays, left preopercular ridge (with ?epibranchial fragment), both hypohyals, a left hypobranchial I, both hypobranchial IIs, both ceratobranchial Is, both ceratobranchial IIs, both ceratobranchial IIIs, both ceratobranchial IVs, basibranchial IV, fused ceratobranchial arch V, ?angular/?supraangular,
BMNH P.11823	405	“Hyomandibulars, branchials etc. (1)”//”Various bones of Leedsia, etc.”	Pair of hyomandibulae, ?left ?parietal, ceratohyal, ?left ?subopercle, bone with large ?nerve canal, 3 hypobranchials, 6 ceratobranchials, 3 epibranchials (2 x I and 1 x II), boss-shaped bone, lepidotrichial fragments (probably non-pectoral)
BMNH P.11824	34	“Gular, epihyal, branchials, etc. (1)”//”Various bones of Leedsia, etc.”	right parietal plus unidentified dermatocranial element (treated) PLUS London material….
BMNH P.11825	20	“Vertebral arches (1)”//”Various bones of Leedsia, etc.”	Robust curved element (used as relative mass indicator ‘34’) plus 12 ?dfs fragments including 5 fairly complete representatives
BMNH P.11826	7	“Fused ditto. (1)”//”Various bones of Leedsia, etc.”	3-way branching ?dorsal fin spine or ?fused supraneural
BMNH P.12534	16	“(3 bones)”//part of 15 fish-remains	left dermosphenotic, odd branched bone plus unidentified dermatocranial element
BMNH P.47412	61	Liverpool specimen - “dissociated bones”	ceratohyal plus lepidotrichial fragment
BMNH P.66340	Alfred Nicholson Leeds (via Liverpool University/Museum)	Leeds ‘11’	left hypohyal, right dentary, ?angular/?supraangular, with unidentified element vaguely similar to ceratohyal
BMNH P.66341	Alfred Nicholson Leeds (via Liverpool University/Museum)	dorsal fin spines (6, including 2 robust curved elements)	
BMNH P.66342	Alfred Nicholson Leeds (via Liverpool University/Museum)	dorsal fin spines (10 - 5 complete)	

Table 2f. Details of *Leedsichthys* specimens, collected by Alfred Leeds, in other museum collections.

Specimen No.	Number of parts	Leeds data	Description
National Museums & Galleries Wales			
NMGW 19.96.G8	68	Leeds no.25	2 hypobranchials, 3 ceratobranchials, left preopercular ridge, pectoral fin rays
National Museums & Galleries Wales			
NMGW 19.96.G9	12		robust curved element ('20'), dorsal fin spines (8, only 1 incomplete)
Kendal Museum			
KMG 1993.72	2	Via ET Leeds	Concretionary nodule with chunk of caudal fin
Museum der Universität Tübingen	2	Via Stürtz	Left parietal, ~420mm long with clump of half a dozen gill rakers on underside
Museum der Universität Tübingen	6	Via Stürtz	Fractured robust curved element ~85mm across {'Fische unbestimmt Malm'}, 2 dorsal fin spines, 1 curved 'hand sickle' element, 1 broken bone callus

Table 2g. Details of miscellaneous other *Leedsichthys* specimens.

Specimen number	Number of parts	Source	Description
BMNH 32581	1	"Branchiostegous rays of fish Oxford Clay - "Dives - Vaches Noire"" from M'sieu Tesson of Caen in 1857.	Concretion of disarticulated gill rakers
BMNH 46355	1	Christian Malford specimen - bought from William Cunningham Esq. in February 1875 - originally figured as reptile ribs?	Isolated fin ray fragment
BMNH P.62054	1	I. Crowson, 1985 Buntings Lane	?pectoral fin rays
Private	1	Alan Dawn Quest Pit, Stewartby	fimbriated tip of dorsal fin spine