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TITLE The fine comb of the Vaches Noire *Leedsichthys* ?

As a researcher, you know the value of collections. Material built up over generations, and accumulated within venerable institutions – always cited and figured, and used as the basis for any state-funded research project. But the role of the private collection is a different one. It is usually acquired through the zeal and tenacity of an individual, without external funding, just their own drive to collect material from a particular locality – sometimes regardless of the prevailing weather conditions.

When I came to research the Jurassic bony fish *Leedsichthys*, I was aware that some of its remains lay in private collections. After all, the original type material had been collected privately, by Alfred Nicholson LEEDS, in the 1880s (SMITH WOODWARD, 1889a). It was one of many animals new to science that he discovered while gathering bones from the many brick pits opened to excavate the Callovian Oxford Clay around Peterborough (LEEDS, 1956). Mostly marine reptiles, many of those animals were named after him by CW ANDREWS (e.g. *Muraenosaurus leedsi*, *Steneosaurus leedsi*), once Leeds' collection had become known to (and bought by) the British Museum (Natural History) in London (ANDREWS, 1910 ; 1913). But the honour of having a genus named after him was reserved for the extremely large bony fish that he discovered **-** *Leedsichthys* (SMITH WOODWARD 1889b) – a suspension-feeding 'prototype'/forerunner of today's basking shark and whale shark. Some may remember that this stunning animal's giant 2.74 metres high tail (FIGURE 1) was mounted in the British Museum until 1987. But since then, no remains of *Leedsichthys* have been on public display in a museum anywhere in the world, apart from the Hunterian Museum in the University of Glasgow, Scotland.

Leedsichthys is a patchy fossil. This is because its skeleton was sparsely ossified, in other words it largely remained cartilage instead of changing into bone as the animal aged, and so it is only partially preserved (LISTON, 2004) – for example, no vertebral centra have been ossified for *Leedsichthys*, a trait that is not unusual within its family, Pachycormidae (LAMBERS, 1992). It has meant that the clusters of isolated bones from it that are found are often misidentified. Over the years, this has resulted in different bones from *Leedsichthys* being incorrectly identified as belonging to a stegosaurian dinosaur on three separate occasions (HULKE, 1887 ; HUENE, 1901 ; MICHELIS et al., 1996).

Of the parts of *Leedsichthys* skeleton that did change from cartilage into bone, many of them contained very limited amounts of bone, with significant resorption of the internal compact bone taking place, often leaving the bones as thin shells or cases, surrounding a largely hollow spongy mass. This means that in bones such as the hyomandibula and parietal, the weight of the surrounding sediment over time has caused the internal spongy bone to collapse, and the bone to be crushed flat. This often leaves the outer shell of the bone fragmented into thin platey shards of bone, with external and internal faces of a bone compressed into tight apposition. Thus even partial remains of the animal will consist not of hundreds, but thousands of parts, consisting of fragments of different layers of different bones, all mixed together. This is one of the reasons that the bones of this animal have remained largely unidentified since its first description in 1889 (SMITH WOODWARD, 1889b).

What would be the possible benefits of such a strategy of restricted ossification of the skeleton? These become clear when one starts to consider the questions of size associated with *Leedsichthys*. Different adult specimens of *Leedsichthys* have been estimated to have lengths ranging from 7-12 metres in length. Growth ring analysis (LISTON et al., 2005) indicates ages ranging from 17 to 31 years, respectively. One specimen, with a calculated age of around 45 years, is likely to be the largest individual of *Leedsichthys* ever discovered, with some of the largest bones known and an estimated size of up to 16.5 metres (LISTON, 2007). These figures indicate a bony fish that lived to large adult sizes, and this would mean a significant body mass. Although weight is less apparent in the aquatic environment, it has significant implications for large animals, which will face problems of constraints on their manoeuverability, in terms of braking, accelerating, turning and sinking. Constraining the proportion of the skeleton that ossifies restricts the skeleton’s density and therefore the fish’s overall body mass. This means that controlling the ossification of the skeleton can help a large animal to travel with less effort through the water column.

Why is it believed that this fish was a suspension-feeder? For one thing, it is utterly toothless. For another, a 1.5 metre long gill basket of this fish has been recovered, lined with a series of elaborate gill rakers (FIGURE 2). Such gill rakers, in conjunction with toothlessness, are closely correlated with suspension-feeding behaviour in contemporary fish, enabling them to suspension-feed on plankton in the water column, as well as filtering the sediment on the sea-bottom, as mammals like grey whales do today (HANS NELSON & JOHNSON, 1987 ; HANS

NELSON et al., 1987). So the specific structure of the gill rakers might well give us important information on the feeding patterns of this animal.

As has been noted, the Oxford Clay in England has been the major producer of the remains of this fish. In addition, it is also found in northern Germany, the Atacama Desert of Chile, and the beaches around Normandie (FIGURE 3). From this last locality, it is exclusively known from the work of private collectors (BUFFETAUT, 1983). In 1857, M'sieu TESSON of Caen sold the British Museum (Natural History) a block of gill rakers (FIGURE 4), identified as the 'branchiostegous rays'of a fish, from the Vaches Noires. For over ninety years, the only element of *Leedsichthys* that was figured in the scientific literature were its gill rakers (SMITH WOODWARD, 1890). Today, the gill rakers of this animal have become a key area of research: after all, if this was the largest bony fish of all time, and it managed to grow so large because of its ability to effectively extract nutrition from the water column, then what was it about its gill rakers, that made it so good at suspension-feeding?

In *Leedsichthys*, the gill rakers resemble small 7.5cm long jaws with an upper serrated edge (FIGURE 5), leading MARTILL (pers. comm.) to briefly believe that he had found a concentration of pterosaur lower jaws when he came across the remains in the Atacama Desert of Chile in the late nineties (MARTILL et al., 1999). In detail, the blocks from the Atacama show hints of a further, finer texture associated with the gill rakers – fragments of a mesh (FIGURE 6 + 7). Although the English Oxford Clay invariably washes easily from the specimens, this softness of matrix also means that it does not support or preserve the fine structures visible in the (slightly younger Oxfordian) Atacama Desert specimens. In contrast, the matrix from the Chilean locality is very hard, but although it preserves the more fragile structures, it is difficult to prepare this material away from this delicate structure without damaging it. Acid-etching starts to reveal some laminae attached to the upper surface of the gill rakers, but even consolidating these structures with Butvar consolidant as they emerge in the acid does not support these fragile elements once more than 2mm of laminar height has been etched from the matrix. State of the art helical CT-scanning has been used at Glasgow's Vale of Leven hospital to try and reveal the three dimensional structure contained within the rock, but it was unable to give the necessary resolution of these fine structures.

I had come across references to the *Leedsichthys* material of CHARLES and PENNETIER in a paper published by Nathalie BARDET in 1993, and I knew that if those collectors had allowed researchers access to their collections before, then they might well do so again (BARDET et al., 1993). In 1993, Bardet's paper had reported the first histological analysis of *Leedsichthys* material, based entirely on ceratobranchial specimens in the collections of CHARLES and PENNETIER. The ceratobranchials are the core component of the fish's gill skeleton, in life supporting the gill lamellae that allow the gas exchange necessary for the fish to respire, and bearing soft tissue to which the gill rakers were attached. These gill rakers sat in the flow of water entering the mouth of the fish, so that nutrient particles (for example, zooplankton such as copepods) would be trapped by them, and redirected towards the fish's gullet. The presence of a further mesh structure sitting on top of the serrated edge of the gill raker hints at an advanced structure for extracting nutrients not previously seen in contemporary or fossil fish.

The German 'ornatenton' *Leedsichthys* material does not contain gill rakers. Could the French material shed some new light on the question of the delicate structures associated with gill rakers? Via the Association Paleontologique and the much-appreciated assistance of Jean Marie GUEGAN, I finally managed to get in touch with Gérard and arranged to meet him with a good friend of mine from Paris, who had kindly offered to act as a translator for me (as, sadly, my French evening classes did not provide me with any lasting availability in this beautiful language). In, 2004 we arrived at the Pennetiers' Parisian domicile, the home of their collection, and I examined the material that they had collected over the years.

The lithology that contained the Pennetier's specimens was indeed different – although the same age as the English Oxford Clay, it acts as a thicker clay matrix, that supports and protects fine structures without being impregnable to the tools of the preparator – in short, just what the researcher needs. This has meant that some exceptional reptile specimens (in particular the skull of a steneosaur) have been recovered and prepared by Elizabeth and Gérard PENNETIER over the years. For the specimens of *Leedsichthys* gill rakers, it was a revelation. One specimen in particular emerged from a nodule, showing its delicate transverse laminae, that seemed to originate just beyond the external gill raker surface before crossing to the matching position on the opposite side of the raker (FIGURE 8). The gill rakers had these delicate planar transverse connections between each side, and possessed a median septum running down the length of the raker. Nothing like this had been seen before for these – or other – fish.

These findings were further supported by remains recovered by private collector Dolf GIELEN from the younger Kimmeridgian age clay of Cap de la Heve in early 2004 (FIGURE 9)

(LISTON, in press). In addition to a series of fin rays, an immaculately-preserved gill raker in his collection (also based in Paris) confirmed the oblique transverse laminae crossing the gill raker. Although these gill raker specimens greatly improve our knowledge of the appearance of undamaged gill rakers of *Leedsichthys*, as opposed to the denuded thousands of gill rakers collected from the English Callovian, they only provide a base for the mesh fragments to sit on, rather than a full three dimensional understanding of the extent of the mesh, and thereby its possible function.

Since the original CT data gathering in November 2004, software has become available that can more effectively discriminate between the delicate structures within the scan images and the surrounding interference patterns from the matrix. Armed with the morphological knowledge gleaned from individual specimens gathered from the beaches of northern France in the collections of PENNETIER and GIELEN, we can hope to use this in conjunction with the scan images to produce a 3D model of a cluster of gill rakers. This model can then be extended to cover the whole of the 1.5 metre long gill basket, in order to assess its likely hydrodynamic activity during *Leedsichthys* swimming and feeding.

Although technology offers many ways forward in extracting data from fossil material, one still needs the high quality fossil specimens – invariably gathered by private collectors – before any such work can be done.

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References

ANDREWS C.W. (1910) - A descriptive catalogue of the marine reptiles of the Oxford Clay. Volume 1. British Museum (Natural History), London, pp 1-205.

ANDREWS C.W .(1913) - A descriptive catalogue of the marine reptiles of the Oxford Clay. Volume 2. British Museum (Natural History), London, pp 1-206.

BARDET, N.; PENNETIER, E.; PENNETIER, G.; CHARLES A. & CHARLES J. (1993) - Des os énigmatiques à 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. *Bull. Trim. Soc. Géol. Normandie et Amis Muséum du Havre*.

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.

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.

HUENE, F. v. (1901) - Notizen aus dem Woodwardian-Museum in Cambridge. — Centralbl. Min. Geol. Pal.: 715-719.

HULKE, J.W. (1887) - Note on some Dinosaurian remains in the collection of A. Leeds Esq., of Eyebury, Northamptonshire. — Quart. Jour. Geol. Soc.London **43**: 695.

LAMBERS, P.H. (1992) - On the Ichthyofauna of the Solnhofen Lithographic Limestone (Upper Jurassic, Germany). - Proefschrift Rijksuniversiteit Groningen: 1-336.

LEEDS, E.T. (1956): The Leeds Collection of Fossil Reptiles. 104 pp. Oxford.

LISTON, J.J. (2004) - 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. (2007) - A Fish Fit For Ozymandias?: The Ecology, Growth and Osteology of *Leedsichthys*(Pachycormidae, Actinopterygii). PhD Thesis. 464 pages.

LISTON J.J. (in press) - The Occurrence Of The Middle Jurassic Pachycormid Fish *Leedsichthys*. *Oryctos*.

LISTON J.J., STEEL, L., & CHALLANDS, T.J. (2005) - Lured by the Rings: Growth structures in *Leedsichthys*. - In: Poyato-Ariza, F. J. (ed.): Fourth International Meeting on Mesozoic Fishes - Systematics, Homology and Nomenclature, Ext. Abstr.: 147-149.

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. — N. Jb. Geol. Palaont. Mh. H 243.

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).]. Geol. Palaont. Westf. **44**: 5.

SMITH WOODWARD, A. (1889a) - On the palaeontology of sturgeons. — Proc. Geol. Assoc. London **11**: 24-44.

SMITH WOODWARD, A. (1889b) - Preliminary notes on some new and little-known British Jurassic fishes. — Geol. Mag., Dec. III **6**: 448-455.

SMITH WOODWARD, A. (1890b) - Note on the gill-rakers of *Leedsia problematica* - a gigantic fish from the Oxford Clay. — Geol. Mag., Dec. III **7**: 292-293.

Comment [MSOffice1]: where's 'a'?

FIGURE 1

The 2.74 metre high tail specimen BMNH P 10000 on display in the British Museum (Natural History), London, in September 1937. Peripheral skeletal components not recovered from the site have been added as a painted backdrop. © The Natural History Museum, London.

FIGURE 2

The 1.54 metre high gill basket of BMNH P.10156 on display in the fossil fish gallery of the British Museum (Natural History) in 1924. Image supplied by Alison Longbottom, NHM (London). 300mm ruler sits in bottom of case for scale. Each branchial arch is flanked by stacks of gill rakers, all preserved in one large concretion.

FIGURE 3

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.

FIGURE 4

Specimen BMNH 32581, a concretion of disarticulated gill rakers from Vaches Noires, the earliest-collected specimen of *Leedsichthys*, sold by Tesson of Caen to Richard Owen of the British Museum (Natural History) in 1857. This specimen was included in Smith Woodward's 1889 type description. Scale bar = 50mm.

FIGURE 5

Lateral view of gill raker in specimen BMNH 32581 (see FIGURE 4), from the Callovian of the Vaches Noires. Width of block in field of view = 129mm.

FIGURE 6

Acid-etched fragment from Atacama Desert block (SMNK2573.PAL), with plan view of fragment, showing 'mesh' etched from surface of limestone matrix, cross-linking from gill raker to gill raker. Fragment = 40mm wide.

FIGURE 7

Outline drawing overlying thin-sections of fragment from SMNK 2573.PAL block, from 'plan view perspective' Interraker gap (distance from centre of gill raker stalk to adjacent centre of gill raker stalk) = 19mm.

FIGURE 8a

Gill raker from Callovian of Normandie, Collection Pennetier. Lateral view showing oblique edges forming transverse planes across the gill raker. Length of gill raker visible = 20mm.

FIGURE 8b

Gill raker from Callovian of Normandie, Collection Pennetier. Plan view of gill raker, showing median septum. Distance between gill raker ends = 60mm.

FIGURE 9

Gill raker from Upper Kimmeridgian of Cap de la Hève. Length = 83mm, Photograph courtesy of D. Gielen.