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The Shock of Unexpected Conservatism: a Counter-signal to Pachycormid Divergence?

J. Liston[1, 2, 3, 4] & A. Maltese[5]

[1] Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Str. 10, 80333 Munich, Germany
[2] Department of Natural Sciences, National Museum of Scotland, Old Town, Edinburgh, Chambers Street, Edinburgh, EH1 1JF, Scotland
[3] Fachruppe Paläoumwelt, GeoZentrum Nordbayern, Friedrich-Alexander Universität Erlangen-Nürnberg, Loewenichstr. 28, 91054 Erlangen, Germany
[4] Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta T0J 0Y0 Canada
[5] Rocky Mountain Dinosaur Resource Center, 201 S. Fairview St, Woodland Park, CO 80863 USA

Corresponding author:
J. Liston
leedsichthys@gmail.com

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Abstract

Pachycormid taxonomy has accepted the twin lineage pattern of toothed and toothless tribes, leading respectively to the Late Cretaceous *Protosphyraena* and *Bonnerichthys*, for over ten years. Recent work on pectoral fin morphotypes has revealed a diversity of forms, reflecting specialization in swimming styles. Examination of pectoral girdle components led to an unexpectedly similar set of characteristics between these two genera, supposedly separated by a gap of over 100 million years since their common ancestor. This raises the question of whether these two taxa are as distantly related as current pachycormid phylogenetic hypotheses suggest.

Keywords: Pachycormidae, *Bonnerichthys*, *Protosphyraena*, *Leedsichthys*, pectoral fin morphotypes

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1. Introduction

Occupying a key-position within Actinopterygii as part of the Holostei-Teleostei Transition, pachycormids are critical to understanding teleost origins. Arising in an explosive diversification in the Toarcian, pachycormids developed into two recognized tribes of 'toothless' (suspension-feeding) and 'tusked' (carnivorous) forms (Liston & Friedman, 2012) persisting until the end of the Cretaceous. As a group they range greatly in size, across three orders of magnitude, exhibiting a trend of reduced ossification for the skeleton with the increasing adult size of a given pachycormid taxon. One of the consequences of this has been the collection of large numbers of isolated pectoral and caudal fins, although little work was traditionally done with them beyond installing them as striking museum showpieces. Recent work on pachycormid pectoral fins has revealed three distinct morphotypes (falciform, gladiform, falcataform) reflecting the wide range of ecology and lifestyles across the group. Thus, all suspension feeders including the Late Cretaceous *Bonnerichthys* possessed the gladiform morph, with *Protosphyraena* and *Australopachycormus* the only genera to have the high aspect ratio falcataform morph. As the effective crown or end-members of the 'tusked' and 'toothless' pachycormid tribes, it was thought unusual in this recent study that *Protosphyraena* and *Bonnerichthys* were geographically and chronologically contemporaneous while occupying adjacent spaces in the PC1 against PC2 plot. According to all recent phylogenetic analyses (Friedman *et al.,* 2010; Schumacher *et al.*, 2016; Dobson *et al.*, 2019) there appears to be a 110 million year gap since the most recent common ancestor of these two genera in the Toarcian, and given the extreme anatomical and physiological (Ferron *et al.*, 2018) developments exhibited within the group during this time, it was determined that the anatomy of the pectoral fin junctions of these two genera should be compared, in order to see how much they had diverged anatomically over this range of time. Although scanning technologies have often produced disappointing results from fossil material in the past (Liston, 2003), the ability of scanning technologies to produce good results from fossil material has improved significantly in the last twenty years (Liston, 2003; Purnell *et al.*, 2006; Dobson *et al.*, 2019) despite some setbacks (Liston & Chapman, 2013) and so it was possible to scan examples of the pectoral fin junction in each genus and manipulate the resulting image data for direct comparison, removing the obstacle of scale.

Recent discoveries of new specimens and innovative preparation work have provided new insight into the three-dimensional shape and arrangement of the pectoral fins in both the tusked and toothless tribes of pachycormids. The unusually long pectoral fins appear to have developed in conjunction with otherwise reduced skeletal ossification to counteract buoyancy problems in a group apparently lacking a gas bladder (see Discussion). Closer analysis also reveals adaptations of a primitive morphology to suit a suite of lifestyles from swift and agile carnivore to slow-cruising suspension feeder. Although a diversity of pectoral fin morphs can be recognised within a group where the pectoral was once simplistically dismissed as ‘scythe-like’, there is a surprisingly high degree of staticity in fin placement and mechanics across both the extremes of these diverse feeding strategies, and 110 million years of geological time. Unsurprisingly, some of the observed pachycormid pectoral fin morphotypes mirror some of the most modern fuel-saving wingtip designs from today’s aerodynamicists, converging on similar efficiency solutions to these enigmatic and fascinating fish.

2. Pectoral fin analysis

As a first step, an overall review of pachycormid pectoral fins was conducted to assess the variability of form, in the wake of the determination that there was no ‘scythe-like’ form that was a synapomorphy for the group. Analysis of shape and aspect ratio across taxa revealed clear differences, not only likely indicators of lifestyle, but also reflecting parallels with modern aerodynamic designs for different functions of aircraft.

In addition to anatomical differences, widely divergent aspect ratios not only gave ecomorphological information, but also helped to define the three distinct pectoral fin morphotypes that emerged (Liston *et al.*, 2019).

The Falceform or ‘sickle’ morph is characterized by a distinctive posterior ‘fillet’, formed by a narrow strip of lepidotrichia at the origin of the pectoral fin, that extends the contact rearward, while tapering distally (Fig.1A). This has the effect of reducing interference drag, increasing the pectoral fin area, potentially as much as doubling the chord length for a given span, and lowering the aspect ratio of the fin (the mean aspect ratio is just under 4 for the Falceform pachycormids studied, Liston *et al.*, 2019). This lifting surface pattern closely matches the wing architecture of the Grumman F-9 Cougar (Fig. 1Aiii), where the long chord near the fuselage junction enhanced low speed lift, important for aircraft carrier operations (Elward, 2010). The Falceform morphology is interpreted as a primitive state, as its representatives are absent after the end of the Jurassic.

The Gladiform or ‘blade’ morphotype lacks the aforementioned fillet, instead featuring leading and trailing edges of the pectoral fin emerging almost parallel at the origin, with an extremely gradual taper to the fin’s tip. The reduced proximal chord increases the aspect ratio relative to a Falceform fin of the same span (a mean aspect ratio of just over 4 is found for the Gladiform pachycormids in the study). A further feature seen in some Gladiform specimens such as *Bonnerichthys* and *Saurostomus* is the presence of an attenuated rearward projecting fin ray at the most distal point of the pectoral fin - ‘processus jagatensis’ – which would appear to assist drag reduction by acting as ‘winglets’ (Fish, 2006) to reduce induced drag of wingtip vortices moving posteriorly across the upper surface of the fin, in order to increase the lift generation at the tips of the pectorals. This vortex shedding structure closely matches that of the Hawker 800 Scimitar winglet, wherein the reduced tip drag being at the end of an ever-longer lever arm means that a less bulky support structure saves energy (El Haddad, 2015) (Fig.1Biii). All suspension-feeding pachycormids possess the Gladiform morph, which is more effective than the Falceform at lower speeds (El Haddad, 2015; Pimentel, 2019), the basic planform being common from the Early Jurassic to the end of the Cretaceous.

The Falcataform or ‘scythe’ morphotype again lacks the expansion at the junction between the fin and the body, the leading and trailing edges extending approximately parallel for the majority of the fin’s length before tapering, sometimes curving posteriorly beyond the point of origin of the trailing edge. The resulting long attenuated shape has a high resultant aspect ratio, the mean value being around 14 in the Falcataform pachycormids studied (*Protosphyraena* and *Australopachycormus*). Ornamentation of the leading edge is common, but not universal – however, it does seem to closely approximate the tubercles on humpback whale flippers, which functionally reduce drag on the biological hydroplane, and main-

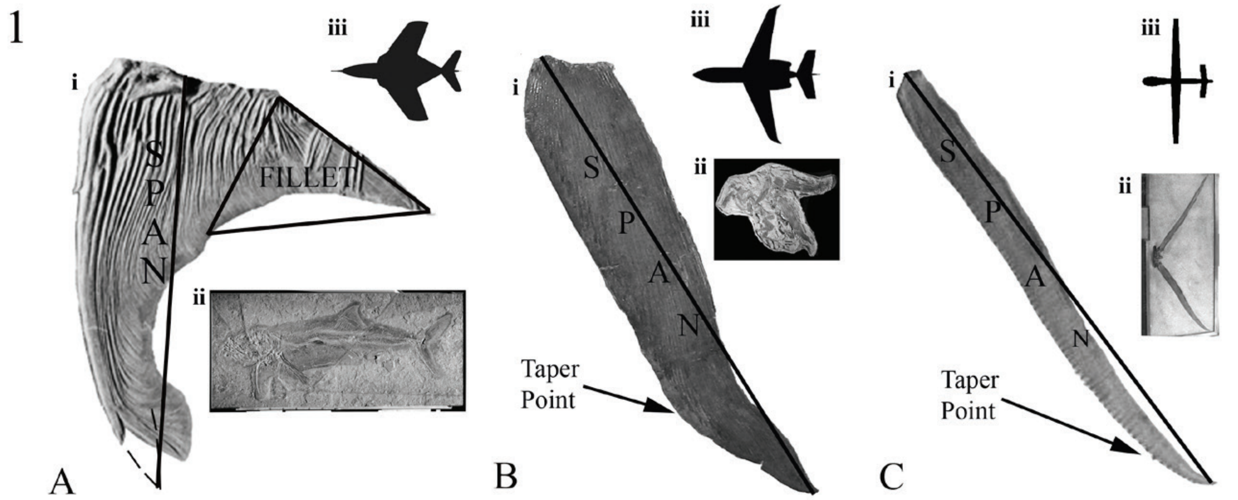

Fig. 1. -The three distinct pectoral fin morphotypes determined within the Pachycormiformes (Liston *et al.*, 2019). In each case, the span line shows the measurement taken for aspect ratio calculation. A - Falceform or sickle morph (i) right pectoral fin of *Saurostomus esocinus* SMNS 56982, detail of full specimen shown in thumbnail (ii) with restored position of fin-tip and fillet structure marked, span length =257mm and (iii) silhouette of the Northrop Grumman Cougar F9 showing the presence of the interference drag-reducing fillet. B - Gladiform or 'blade' morph (i) right pectoral fin of *Bonnerichthys gladius* FHSM VP-17428, detail of full specimen shown in thumbnail (ii) with point of transition from gradual to accelerated taper indicated; span length =614mm long, and (iii) silhouette of the Hawker 800 Scimitar showing the presence of the vortex-shedding scimitar. C - Falcataform or 'scythe' morph (i) right pectoral fin of *Protosphyraena perniciosa* FHSM VP-80, detail of full specimen shown in thumbnail) with point of transition from parallel to acute taper indicated, span length =1040mm, and (iii) silhouette of the General Atomics MQ-9 Reaper Drone for comparison. Silhouettes depict plan views of aircraft with equivalent wing planforms, representing convergence of aeronautical engineering designs on pachycormid pectoral fin shape. Figure by JJ Liston, from silhouettes by JJ Liston and photographs by R. Böttcher, Anthony E Maltese, Mike Everhart.

tain lift at high angles of attack (Fish & Battle, 1995; Fish *et al.*, 2011). Falcataform fins are ubiquitous on Cretaceous pachycormid pursuit predators, the high aspect ratios indicating a high degree of maneuverability, especially in tight turns. This wing planform is close in form to the General Atomics MQ-9 Reaper Drone (Fig.1Ciii), optimized for long periods of moderate-speed cruising. Other aircraft such as the swing-wing fighters (MiG-23, F-14 Tomcat) extend their high aspect ratio wings during turning combat for increased agility (Kress & Gilchrist, 2002).

With this classification in place, a clear pattern emerged of fin form reflecting niche specialisations, and reflecting the 'two tribes' structure previously established within pachycormids (Liston & Friedman, 2012), specializing towards pursuit predator and large suspension-feeder forms, the split between them believed to have taken place no later than the Toarcian in the Early Jurassic. Thus, in Toarcian specimens both Falceform and Gladiform are present with Falceform being dominant, but this dominance is reversed by the Late Jurassic. For most specimens, only two dimensional examination of complete fins was possible, although some less complete three dimensionally preserved pectoral fins are known for *Bonnerichthys* (showing a symmetrically cambered hydrofoil in cross-section, giving good stability) and *Leedsichthys* (a deep cambered fin profile for high lift at low speeds). Recently, an opportunity arose to compare the end Cretaceous representatives of each of these, via a couple of unusually-preserved specimens. The first near-complete specimen of *Protosphyraena* ever found (RMDRC 03-005) in almost 200 years (Liston, 2015) has given new information about this taxon (again reflecting the fragmentary nature of the skeletal remains of these animals, with declining ossification), measuring 2 metres Standard Length (SL) with its Falcataform pectoral fin, exemplifying the pursuit predators. For detailed understanding of the pectoral girdle, another specimen was used for preparatory dissection of the relevant structures (FHSM VP-18957). The second specimen examined was a 4-5 metre long *Bonnerichthys* (RMDRC 11-036) for the suspension-feeders, with Gladiform pectoral fin. With an intervening period of over 100 million years of fin specialization, it was decided to examine the internal structure of the pectoral girdle of these two animals, to determine the nature of joint adaptations that had occurred to refine their movement control. In order to act as guidance, the skeletal remains of the 9-12 metre long Middle Jurassic pachycormid suspension-feeder *Leedsichthys* (Liston, 2010; Liston *et al.*, 2013) were included for reference.

3. Material & methods

Bonnerichthys: KUVP 60692 scapulocoracoid; RMDRC 11-036 radiale II; FHSM VP-17428 pectoral region;

Protosphyraena: radiale II from FHSM VP-18957; RMDRC 16-039 scapulocoracoid; RMDRC 03-005 a near complete individual (*P. tenius*);

Leedsichthys: NHMUK P6921 radiales; PETMG radiale I (left, 199mm long, PETMG F.174/245) and radiale II (right, 250mm long, PETMG F.174/263) from the right pectoral fin.

The *Bonnerichthys* scapulocoracoid (KUVP 60692) was just under 300mm long, while the slightly damaged *Protosphyraena* scapulocoracoid (RMDRC 16-039) was just under 50mm long. Given the large differences in size (similarly, the height of radiale II of *Bonnerichthys* RMDRC 11-036 was almost four times the height of the *Protosphyraena* radiale II FHSM VP-18957) all elements were scanned using a NextEngine or Artec Spider 3D Scanner and rendered utilising ScanStudio 2.02 or Artec Studio 13 software visualized in MeshLab, in order to print out enlarged versions of the bones and physically manipulate them for more easy direct comparison of physical form. Attention was focused on common areas, undamaged by breakages or taphonomic bending.

4. Results

Although previously noted that the pectoral girdle anatomy of *Bonnerichthys* "corresponds to that found in other pachycormids" (Friedman *et al.*, 2010, Supplement, p.17), under close examination, the articular sockets for the radiales of both animals are remarkably similar (Fig. 2), with the same pattern of a relatively small triangular first socket followed by three dorsoventrally longer slightly curved crescent-like sockets being followed in both cases. Similarly, the pectoral knob occupies a similar anterodorsal position with respect to the first radiale socket in terms of its proportional location in relation to the sockets. However, a critical difference lies in those sockets, with the presence of an hemiradial septum in each of sockets I-V distinguishing the two genera. The effect of the septum is that for all socket articulations except the first two, *Bonnerichthys* has two discrete radials for every one of *Protosphyraena*, meaning that it has close to double the compliment of radiales in its scapulocoracoid compared to *Protosphyraena.*

Examination of the most complete specimen of *Protosphyraena* known – the juvenile RMDRC 03-005 – gives an indication of why this disparity exists: fusion lines are visible in some of the radiales present (Fig. 3), suggesting that the paired hemiradiales that share each socket fused in antero-posterior order. This observation is consistent with previous work noting the likelihood of a paedomorphic explanation for the trend of reduced proportion of skeletal ossification with increased size of any given adult pachycormid taxon (Liston, 2004; Liston *et al.*, 2013), as well as the lack of segmentation in pachycormid fin rays (Liston, 2007) and reduced scale cover (Liston, 2007).

The radiale II is the largest of the radiales in both genera, and strikingly similar in their crudely reniform shape with indentation to receive the pectoral knob of the scapulocoracoid, and dual scapulocoracoid articular facets. Indeed, in comparing the radiale

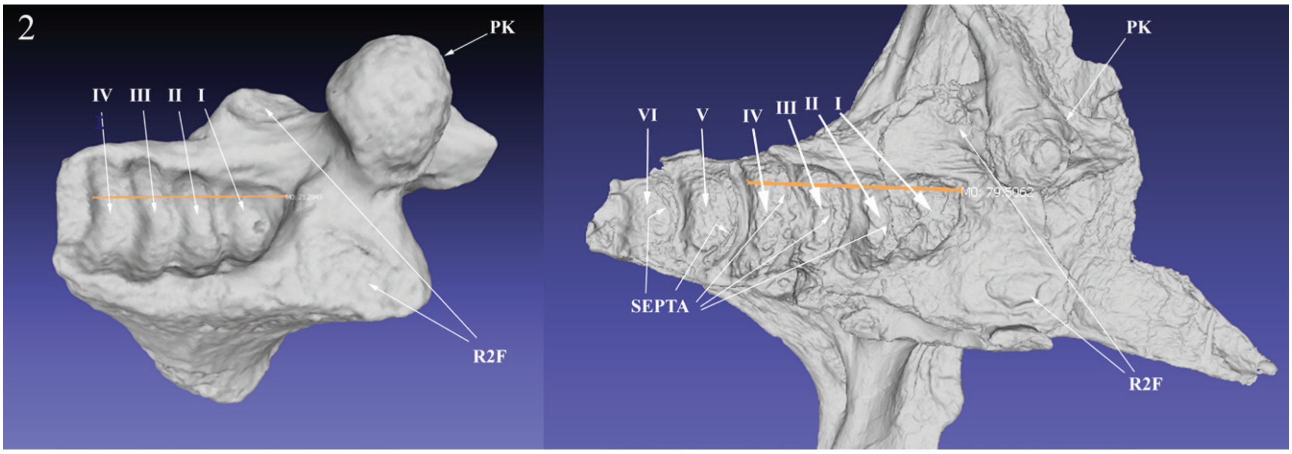

Fig. 2. -Comparison of lateral views of scapulocoracoid sections from *Protosphyraena* (L) RMDRC 16-039 and *Bonnerichthys* (R) KUVP 60692, magnified to corresponding sizes for comparison, imaged in Meshlab. Distance from anteriormost point of radiale articular socket I to rear of radiale articular socket IV shown in orange on each (*Protosphyraena* 21.3mm, *Bonnerichthys* 79.5mm). R2F= articular facet for radiale II; PKA= pectoral knob; I-VI= articular sockets for radiales I-VI; septa = hemiradial septa in articular sockets of *Bonnerichthys*.

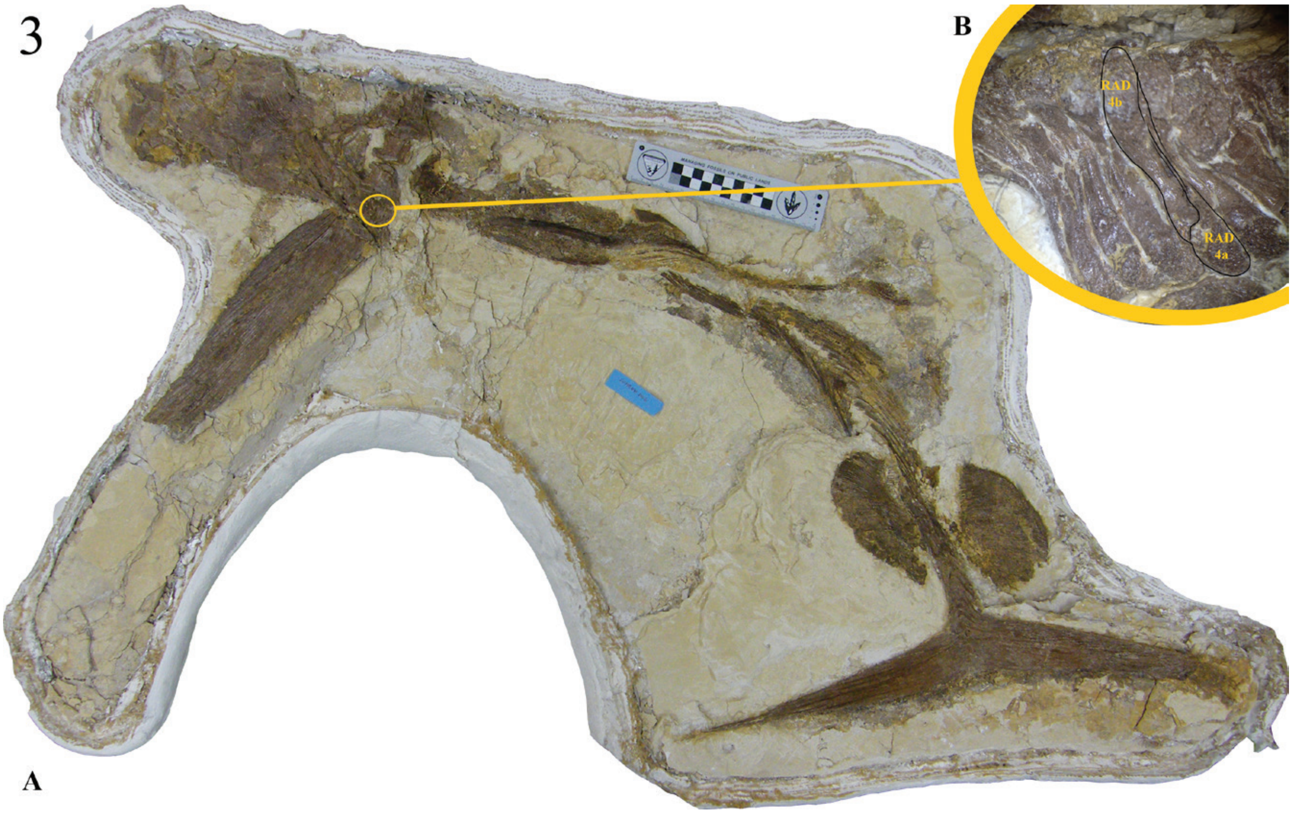

Fig. 3. -A - Complete specimen of juvenile *Protosphyraena tenius* (RMDRC 03-005) with location of detail (B) marked on it. Radiales show fusion taking place between hemiradiales. RAD 4a= anterior hemiradiale 4; RAD 4b = posterior hemiradiale 4. Field of View 40mm.

II of both *Protosphyraena* and *Bonnerichthys* (Fig. 4), aside from the difference in size, the degree of crushing is the most striking physical difference between the two (Fig. 5). As has been noted elsewhere, this appears to be a consequence of the previously noted phenomenon of reduced ossification in pachycormid taxa with large adult size (Liston, 2010; Liston *et al.* , 2013), wherein the extensive degree of bone resorption leaves the remains of the larger taxa far more vulnerable to crushing during sedimentary compaction, as seen in many bones of the even larger suspension-feeding pachycormid *Leedsichthys* (Fig. 6),

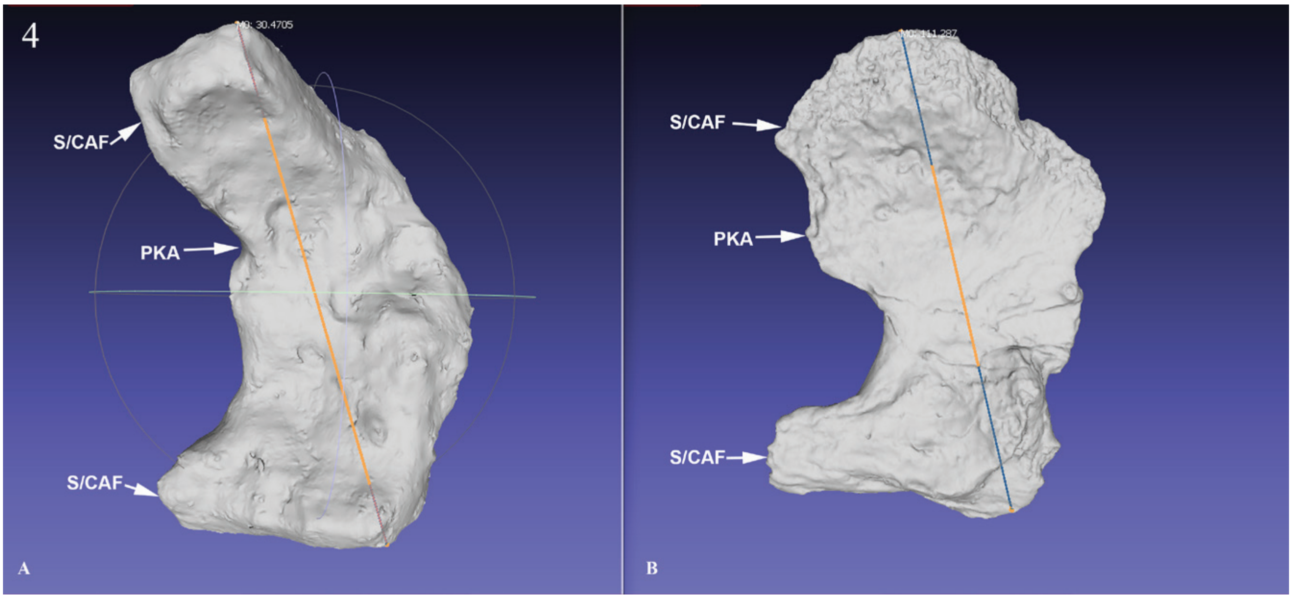

Fig. 4. -Comparison of lateral views of radiale II from *Protosphyraena* (L) FHSM VP-18957 and *Bonnerichthys* (R) RMDRC 11-036, magnified to corresponding sizes for comparison, imaged in Meshlab. Distance from superiormost to inferiormost points shown in orange on each (*Protosphyraena* 30.5mm, *Bonnerichthys* 111.3mm). S/CAF=scapulocoracoid articular facet; PKA= location of site of articulation with pectoral knob.

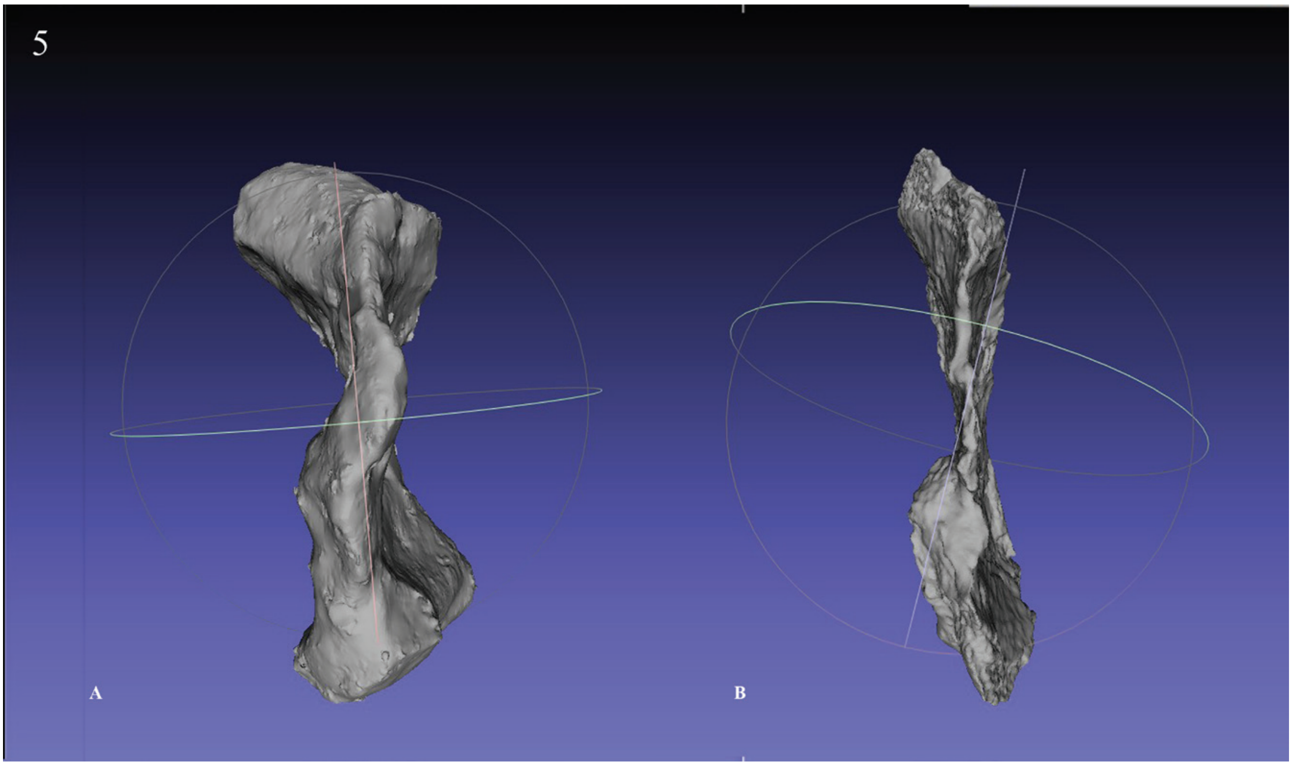

Fig. 5. -Comparison of views of medial edges of radiale II in *Protosphyraena* (L) FHSM VP-18957 and *Bonnerichthys* (R) RMDRC 11-036, magnified to corresponding sizes for comparison of anteroposterior crushing, imaged in Meshlab. For scale, see previous figure.

which had a high degree of bone resorption throughout much of its ossified skeleton, resulting in most of its bones being crushed flat (and often fragmented) during compaction. Perhaps significantly, despite their large size, no more than two radiales have ever been found associated with the remains of a single individual of *Leedsichthys* (Liston, 2007).

In short, the fusion visible through juvenile and adult specimens of *Protosphyraena* is delayed in *Bonnerichthys*, leaving a larger number of radiales, bones that, instead of being the robust solid compact bone in *Protosphyraena*, would have been full of cancellous bone. This is reflected by the degree to which the radiales have been vulnerable to crushing during sedimentary compaction in the larger suspension-feeding *Bonnerichthys* (Fig. 7). This combination of resorption and suspension of fusion is a mechanism by which the biological strategy of mass minimisation through compact bone reduction continues in the pectoral fin joint, without compromising the strain resistance of the radiale unit itself, through doubling the number of compact layers of bone present in the socket at the level of the hemiradial septum. The stress resistance from the compact bone is being preferentially concentrated in the vertical plane, which is why this crushing is visible in this unidirectional flattening. It is proposed that this is an evolutionary means of compromising the degree of bone resorption required throughout the animal's skeleton, with not reducing the length of the radial groove required for the articulation of such an extensive pectoral fin.

Considering the diversity of fin types and the anticipated evolutionary divergence point of these two lineages of extremely specialized swimmers, it is surprising how much the patterns of articular sockets in the scapulocoracoids of *Protosphyraena* and *Bonnerichthys* physically resemble each other, implying an unexpectedly large degree of conservatism between these two taxa.

5. Discussion

5.1 Pachycormid Taxonomy and Buoyancy Adaptations: The Need for Wing-like Pectoral Fins in Pachycormiformes.

The buoyancy adaptations of pachycormids can be viewed as the core driver for the major skeletal modifications that have been used to define the group, whether as 'microlepidoti' (Wagner, 1851; Heineke, 1906) where overall body mass is reduced through reduced scale dimensions, including thickness, the reduced ossification of the postcranial skeleton with the increasing adult size of the taxa, or their wing-like pectoral fins so reminiscent of those of swim bladder-less cartilaginous fish. These adaptations have in turn traditionally drawn the attention of taxonomists seeking to group pachycormids as discrete, characterizing them primarily through their buoyancy requirements. It is within this context that the refinements of the pectoral fins to be large lifting surfaces should be viewed, whether for slow-feeding suspension feeders or high speed pursuit predators, which represent the extreme ends of the pachycormid lifestyle continuum

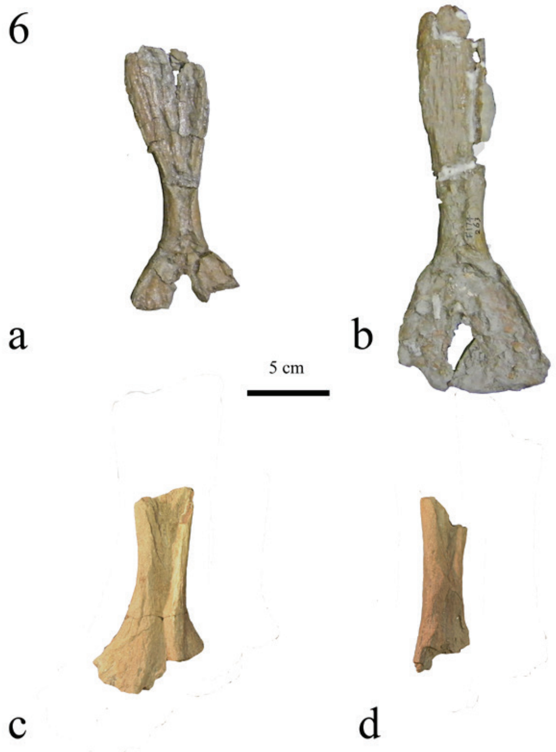

Fig. 6. - Radiales of *Leedsichthys*, in the 'Ariston' (PETMG F174) and holotype (NHMUK P.6921) specimens, showing crushing. Radiale I (a, 199mm long, PETMG F.174/245) and radiale II (b, 250mm long, PETMG F.174/263) from the right pectoral fin. Radiale II (c, 118mm long) and radiale I (d, 101mm long) from NHMUK P.6921. Scale bar = 50mm. (Layout by FM Holwerda, after figures 8.43 and 8.44, Liston 2007)

The earliest descriptions of the Family Pachycormidae (Woodward, 1895) refer to the characteristics of the group that indicate adaptations towards efficient swimming: in addition to more conventional traits shared by other bony fish (a streamlined body and a lunate or semilunate tail) there are the four far more unusual features of the disproportionately long pectoral fins, reduced skeletal ossification, reduced body scales and an unusually high number of notochord segments (compared to their contemporaries) providing better potential flexion of the tail during movement. Excepting the last characteristic, the first three would significantly ease problems in achieving neutral buoyancy. The disproportionately long pectoral fins (described by Woodward as 'tactile organs' (Woodward, 1916), and which led to them being nicknamed 'vogelfisch' Liston *et al.*, 2019) provided greater lift, and it has been noted that the possession of wing-like pectoral fins by cartilaginous fish is in particular to compensate for their lack of swim bladders, through giving additional lift from the pectoral fins. The detail of the scapulocoracoid sockets also indicate that – as with cartilaginous fish – the pectoral fins of these pachycormids could not be retracted to be flush with the body, as with teleosts, so would perpetually be in the slipstream and having an active impact on altitude control as the animal moved forward. Similarly, the reduced skeletal ossification would have acted to reduce the density of the fish (as it does with the secondarily derived cartilaginous skeleton of the heaviest teleost, *Mola mola*, Freedman & Noakes, 2002, due to the lower density of cartilage) and therefore the work required to achieve neutral buoyancy, as would the reduction of body scales (ultimately leading to their complete disappearance with the increasing size of the adult taxon), along with acting to reduce drag over the surface of the body. The reduced skeletal ossification with increasing size of adult pachycormid taxon has the interesting effect of showing an unusual craniate direction of ossification in pachycormids (Liston *et al.*, 2019), as specimens with only some of their vertebral centra ossified universally have the caudal centra preserved with the more cranial centra absent (e.g. Liston *et al.*, 2019, Fig. 8). It has been speculated previously that the swim bladder, as a mechanism that aids the animal to achieve neutral buoyancy, might be a specifically teleost trait (Freedman & Noakes, 2002), Although it has been argued that pachycormids were not teleosts (Arratia & Schultze, 2013; Schultze & Arratia, 2013) and as such would have been exempt from such a criterion, it is nevertheless the case that, even within Teleostei, examples exist of bony fish that have reduced or entirely lost their swim bladders (e.g. Scomber, tuna, Bone, 2009). This is specifically noted as advantageous for fish that have large vertical migrations, in some cases using lipids rather than gas in their swim bladders (e.g. the sunfish *Mola mola* and myctophids, both of which migrate hundreds of metres daily following their prey of, respectively, jellyfish and copepods, Freedman & Noakes, 2002)

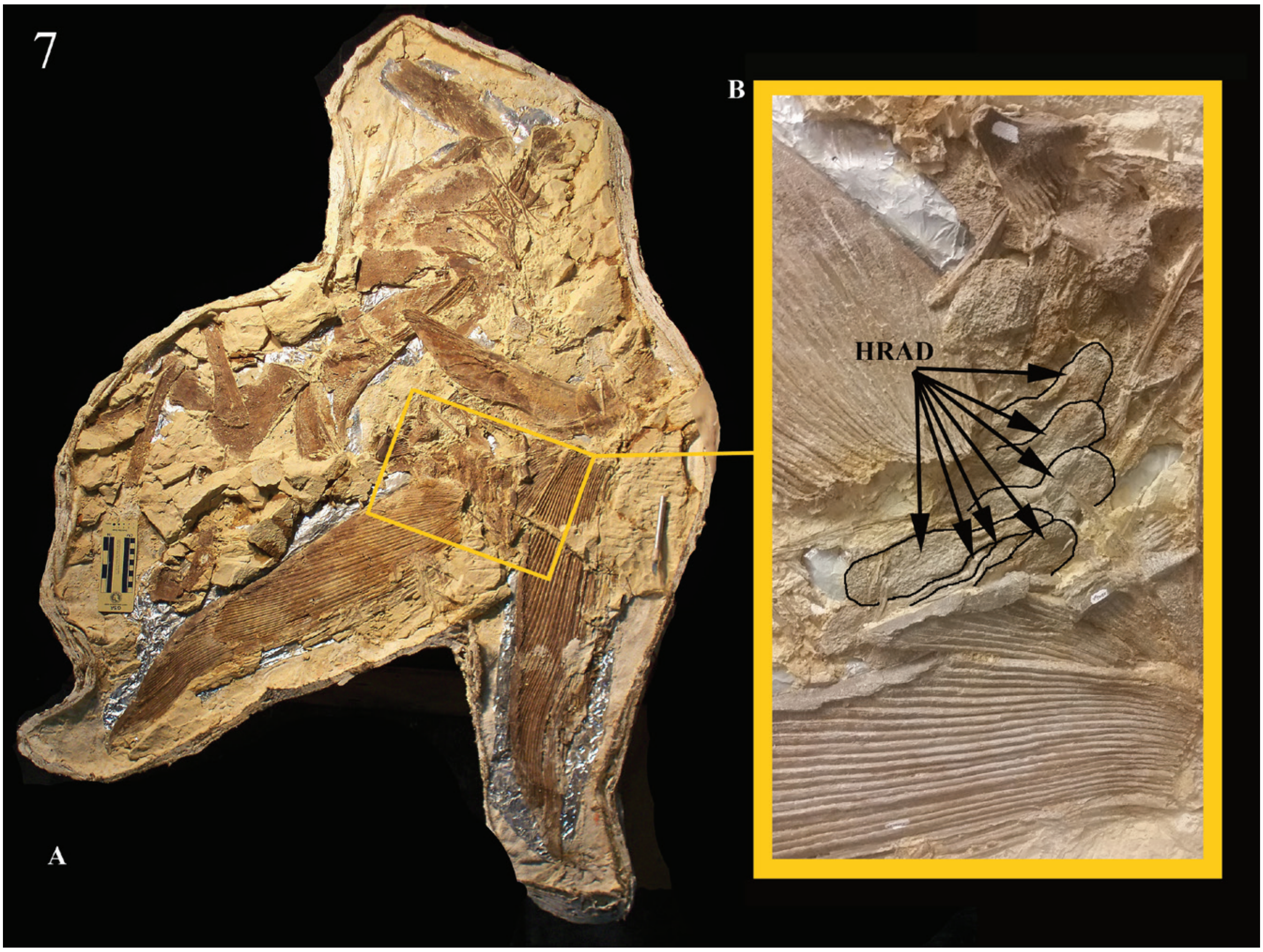

Fig. 7. -(A) complete specimen of *Bonnerichthys gladius* (FHSM VP-17428) – with location of detail (B) marked on it. HRAD = Hemiradiales;

as a swim bladder generally can be limiting in terms of the size of the migratory range undertaken by an animal (Bone, 2009). This is particularly noteworthy in the context of the pachycormids that were the first large (>1 metre Standard Length) suspension-feeding vertebrates, growing up to some 16 metres in length. Their suspension-feeding apparatus seems well-adapted for zooplankton the size of copepods (Liston, 2007), which emerged as a dominant planktonic form during the Triassic (Bone & Marshall, 1982; Freedman & Noakes, 2002) and are noted as having significant diurnal ranges of up to hundreds of metres in the present day (Baumgartner *et al.*, 2011).

When one considers that a swim bladder acts to assist the fish in achieving neutral buoyancy, and occupies between 5 and 12% of body volume, depending on bone density and degree of scale density (Bone, 2009), it gives some pause for thought that applying Webb (1975) to the most conservative estimates of *Leedsichthys* size (Liston, 2007) would indicate a swim bladder volume of around 500 litres. The impracticality of such an organ, especially in an animal pursuing diurnally migrating prey over more than a hundred metres, in conjunction with the above-noted buoyancy adaptations, do strongly argue that pachycormids lacked swim bladders.

5.2 Outstanding Issues of Taxonomic Uncertainty in Pachycormiformes.

Although recent new discoveries in the Toarcian of Scotland, as well as the Kimmeridgian and Turonian of North America (Blanco-Piñón *et al.*, 2002), have expanded our global knowledge of the diversity, distribution and success of pachycormids, continuing the recent ‘Pachycormid Renaissance’ that has doubled the number of genera assigned to the group over the last thirty years, the Toarcian (Lower Jurassic) Holzmaden and Kimmeridgian-Tithonian (Upper Jurassic) Solnhofen plattenkalk faunas remain the main sources of information about these animals. Recent comparative work has revealed how poorly constrained a number of historical genera such as *Pachycormus*, *Sauropsis* and *Euthynotus* are: originally described by Agassiz (1833-1843) and de Blainville (1818), these taxa were the foundation of Arthur Smith Woodward's Family Pachycormidae in 1895 (Woodward, 1895). In addition, clarity over the definitions of pachycormid taxa (as with many other fossils) have not been improved due to the number of type specimens destroyed during World War II, which introduced a need for Neotype material to be identified for *Asthenocormus titanius* and *Hypsocormus macrodon* (Lambers, 1992) as well as *Protosphyraena tenuis* (Liston *et al.*, 2019). Furthermore, reviews of group-level characters demonstrate that the presence of rhombic scales and a 'scythe'-like pectoral fin are not pachycormid synapomorphies (Liston *et al.,* 2019). Finally, the trend towards reduced ossification with increasing adult-size of a taxon means that much of the skeleton in many taxa is simply not preserved, hampering the preservation of many characteristics used to code other actinopterygians. It is evident that this group requires a long overdue large-scale systematic overhaul in order to stabilise it (Liston, 2008).

Lambers began the process of this overhaul with his thesis work in 1992, establishing a neotype for *Asthenocormus*, and setting the baseline for a broad cladistic analysis of the pachycormids (Lambers, 1992). *Hypsocormus macrodon* similarly requires the establishment of a Neotype, as well as clarification of its definition, as it appears distinct from *Hypsocormus*. Recently, Wretman *et al.* grasped the thistle of *Pachycormus*, with the poor (and missing) type specimens for its species as well as the limitations of the original definition (Wretman *et al.*, 2016). *Euthynotus* and *Sauropsis* each have species that may well prove to be distinct genera, and so require a similar reassessment to Wretman *et al.'*s.

Problematic analyses arise from these poor definitions for the group, the genera and the species. For example, Hurley *et al.'*s 2007 analysis used only one pachycormid – *Pachycormus* – without stating which species. Friedman *et al.* (2010) then used the Hurley *et al.,* 2007 database to expand an analysis of Pachycormidae, with highly variable coverage (three individual species of *Hypsocormus*, yet agglomerations of '*Pachycormus* sp.', '*Orthocormus* sp.', '*Protosphyraena* sp.' and '*Euthynotus* sp.' are also incorporated). These broader analyses have not only omitted many taxa, but have condensed extremely diverse species into single genera, and even expected those genera to carry a signal for the group as a whole, when even the most basic of characters is poorly defined and coded for. When it is not clear exactly what *Pachycormus* or any individual genus actually is, or which species of that genus is being referred to, it is hard to have confidence in it being used within an analysis, especially given the quantity of missing data involved (Arratia & Schultze, 2013), reflecting the shortage of data amongst many of the skeletal remains of these ossification-restricted taxa. The vagueness has also impacted on descriptions of new taxa, the definition of *Rhinconichthys* requiring a complete overhaul within five years of its original description (Schumacher *et al.*, 2016).

In the context of this taxonomic flux, the apparent similarities between *Protosphyraena* and *Bonnerichthys* were assumed to be convergence in Dobson *et al.* (2019), but this must be considered with some caution in the light of the apparent similarities in scapulocoracoid articular sockets as well as pectoral fin ray arrangement, pelvic fin character and gill raker form between these two Cretaceous taxa.

5. Summary of conclusions

The traditional descriptor of 'scythe' or 'sickle' shaped is observed to be flawed as an effective descriptor for pectoral fin shape in pachycormids, therefore the diversity of pachycormid pectoral fin shapes has been assessed, and improved terms defined to more effectively describe their form, supported by aspect ratio analysis of individual fins. Camber interpretation in rare uncrushed pectoral fin specimens support lifestyle interpretations. Variations due to the presence of the scapulocoracoid's hemiradial septum in *Bonnerichthys* is interpreted as consistent with the demonstrated strategy of compact bone reduction with increased adult size. Despite the extremes of fin shape in *Bonnerichthys* and *Protosphyraena* reflecting diversity of lifestyle, the radial fin attachment architecture is surprisingly conservative, considering the large degree of presumed evolutionary separation.

This new data allows us to apply these inferences to animals that, through a pronounced lack of skeletal ossification, would otherwise remain more mystery than organism.

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