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Daggers, swords, scythes and sickles: Pachycormid fins as ecological predictors

Pachycormids occupy a key position within Actinopterygii, as part of the Holostei- Teleostei Transition, although their precise position in this hierarchy has been fought over for some years. Discoveries in the last three years have expanded our global knowledge of the diversity, distribution and success of this group, continuing the recent 'Pachycormid Renaissance'. However, clarity over the definitions of pachycormid taxa has been undermined by the number of type specimens destroyed during World War II, introducing a need for neotype material to be identified (e.g. Asthenocormus titanius, Hypsocormus macrodon), and comparative work has revealed how poorly constrained a number of historical genera are, particularly those of the Toarcian (Early Jurassic) Holzmaden shale fauna that were the foundation of Arthur Smith Woodward's family Pachycormidae in 1895. These historical problems with descriptions and material have undermined confidence in recent phylogenetic analyses. The characteristic unusually long pectoral fins appear to have developed in conjunction with otherwise reduced skeletal ossification to counteract buoyancy problems in a group lacking a gas bladder. A sample of over 90 specimens from 16 recognised pachycormid genera was assessed, demonstrating that the ubiquitously stated 'scythe'-like pectoral fin is not a pachycormid synapomorphy: three clear and distinct pectoral fin structural morphotypes emerged, reflecting a diversity of pachycormid lifestyles that changed throughout the Mesozoic, from agile pursuit predator to slow-cruising suspension feeder. Those morphotypes closely mirror modern fuel-saving wingtip designs from today's aerodynamicists, converging on similar solutions to these enigmatic and fascinating fish some 160 million years later.

DAGGERS, SWORDS, SCYTHES AND SICKLES: PACHYCORMID FINS AS ECOLOGICAL PREDICTORS

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Asthenocormus, BaJ2344

Bonnerichthys, KUVP-465

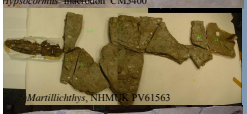

Euthynotus, 10638


Haasichthys, Tu228


Hypsocormus, AMNH 7487


Leedsichthys PETMG E174, right pectoral fin.


Hypsocormus macrodon CM5400


Martillichthys, NHMUK PV61563


Orthocormus, JME-SoS3571


Pachycormus, G 338-1894


Pachycormus, uniquely anomalous falcataform IRSNB Vert-00-133.


Australopachycormus (Cdz.) NHMUK PV P.73611


Absentee Author B: Still lost, Miles away in a muddy river in Ecuador.

INTRODUCTION

Pachycormids occupy a key-position within Actinopterygii, as part of the Holostei-Teleostei Transition, their precise position in this hierarchy having been disputed for some years. However the group remains highly problematic due to a large number of historical problems with both descriptions (poorly defined genera and species) and material (holotypes based on incomplete, missing or destroyed specimens), which undermines confidence in recent phylogenetic analyses. The issue relating to material is deeply affected by the trend within the group for reduced skeletal ossification, particularly concerning their body scales and vertebrae (arcocentra and chordacentra), which can severely compromise the cohesiveness and thus the collectability of some Jurassic and many Cretaceous taxa.

It has previously been noted that Patterson was the first to erroneously state that pachycormids have a ubiquitous 'scythe'-shaped pectoral fin, in direct contradiction of Arthur Smith Woodward. This work aims to demonstrate the wide variability of pectoral fin shape with pachycormid taxa, reflecting a range of ecological spaces occupied by the members of this family, through comparison of aspect ratio, and finally define useful categories for describing and defining this variability in pectoral fin shape.

MATERIALS & METHODS

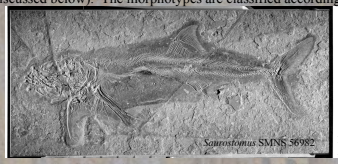
Specimen selection

80 pachycormid specimens with at least one well-preserved pectoral fin, and covering all recognised pachycormid genera (bar *Rhinconichthys* and *Neopachycormus* neither of which have full pectorals preserved) were selected, ranging from the Toarcian to the Campanian in age. This study was initiated to assess the degree of variability in pectoral fin planform across (and within) pachycormid taxa, using hydrodynamically relevant parameters. It was anticipated that pectoral fins would have forms with hydrodynamic properties reflecting the niches and lifestyles of the individual taxa. Pectoral fins were examined in terms of their surface area and aspect ratio. As postcranial variability within the genus *Pachycormus* had been identified as unusually large by LISTON (2007), this genus was particularly intensively sampled (forming around a third of the specimens), in an attempt to bring to light any possible underlying anatomical patterns that might indicate a degree of taxonomic diversity outwith the current recognised species of *bollensis*, *macropterus* and *curtus*. Photographs were processed using ImageJ, data processed in Microsoft Excel and OpenOffice Calc.

RESULTS

Discrete clusters emerged for three groups of pectoral fin morphotypes, with corresponding aspect ratio (AR) values. Genera tended to be morphotype specific, with few exceptions (discussed below). The morphotypes are classified according to the following descriptions:

Type 1 Falceform or 'Sickle' morph


Saurostomus SMNS 56982


Isolated fin from SMNS 56982.


Sickle


Grumman F-9 Cougar

Pectoral fins that possess a distinct posterior fillet at their proximal boundary. This fillet consists of a narrow strip of lepidotrichia at the origin of the pectoral fin, projecting rearward and tapering along the junction with the body. Functionally such a structure reduces interference drag by extending and smoothing the perpendicular junction of the pectoral fin, as well as increasing the pectoral fin area by as much as doubling the chord for a given span. This lowers AR, with the sample group having a Mean (average) value of 3.99 (Mode of 3-4, Median of 3.58). *Saurostomus esocinus* SMNS 56982 is the designated archetype for falceform fins. We interpret falceform morphology as a primitive state, representative specimens ceasing to appear in the fossil record subsequent to the Late Jurassic (Kimmeridgian-Tithonian of Solnhofen). Aerodynamically, the fillet can be seen in the Grumman F-9 Cougar.

Type 2 Gladiform or 'Blade' morph


Bonnerichthys, FHSM VP-17428


Isolated fin from KUVP-465


Kitchen knife

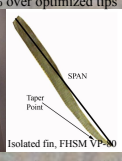

Extended 'winglet' pectoral ray on *Bonnerichthys* FHSM VP-17428-03

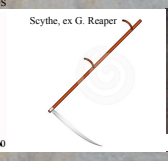

'Winglet' on Hawker 800 wingtip.

Pectoral fins lacking substantial proximal posterior expansion at the fin-body junction. Anterior and posterior margins nearly parallel at origin, tapering quite gradually but constantly to the distal tip. Reduced proximal chord results in a higher AR fin, with the sample group displaying a higher Mean (average) value of 4.45 (Mode of 4-5, Median of 4.37). *Bonnerichthys gladius* KUVP 465 is the archetype for gladiform fins. These fins are generally broad, of the type previously referred to as a tightly-bound series of parallel sticks for *Asthenocormus* as well as other as yet undescribed suspension feeding pachycormids (LISTON 2008, LISTON & FRIEDMAN 2012, LISTON et al. 2012). All suspension-feeding pachycormids fall within the gladiform morphotype, with the basic planform common from the Early Jurassic until the very end of the Cretaceous. Within this group, *Bonnerichthys* also preserves an attenuated leading pectoral fin ray orientated backwards and extending beyond the margin of the trailing edge of the fin. Arguably this extended ray may have acted like winglets on a Hawker 800, with drag reduction achieved from the tip vortex moving from the top surface of the fin rearward to an area slightly behind the tip. In this context it is worth noting that although in aircraft design this structure achieves similar drag reduction to the Type I fillet, the Type II tip structure is more effective at relatively lower speeds, where it can improve efficiency by 5-7% over optimized tips

Type 3 Falcataform or 'Scythe' morph


Protosphyraena, RMDRC 03-005


Isolated fin, FHSM VP-80


Scythe, ex G. Reaper

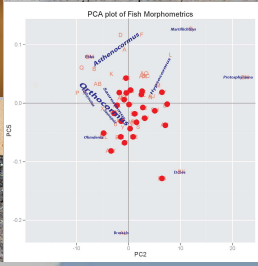

RQ4A drone

Lacking substantial proximal posterior expansion at the fin-body junction, the leading and trailing edges extend roughly parallel distally for the majority of the fin length before tapering, sometimes curving posteriorly beyond the trailing edge origin point. Though not universal, leading edge ornamentation is common. The long slender shape results in an exceptionally high AR with a Mean (average) value in the sample group of 13.48 (Mode of 14-15, Median of 13.59), with the archetype *Protosphyraena perniciosa* FHSM VP-80 attaining nearly 15. Falcataform fins are ubiquitous on Cretaceous pachycormid pursuit predators, where high aspect ratios enable a high degree of maneuverability especially in tight turns. The aerodynamic equivalent in planform terms is the RQ4A-type 3 endurance drone, with an aspect ratio of 12.5.

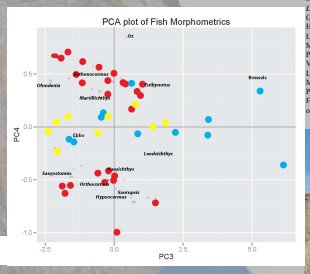
The aspect ratio range and morphotype of each genus was found to be conservative and well constrained, except in the case of *Pachycormus*, where they were found to be unusually wide-ranging (one third falceform, two thirds gladiform, and even one falcataform example). This variation is independent of SL, therefore is interpreted as a wider ecological and possibly taxonomic disparity within the genus, than is currently recognised.

PRINCIPAL COMPONENT ANALYSES

Two Principal Component Analyses exercises were conducted on the data using 'R', separating complete specimens (i.e. those for which the Standard Length could reliably be measured for the purposes of comparison with pectoral fin length and body position) from incomplete. Within the complete specimen analysis, pectoral fin position and aspect ratio most accurately recovered the currently recognised genera, with *Pachycormus* split into two discrete groups. Similarly, for partial specimens, aspect ratio and fin type most faithfully recovered clusters of the currently recognised genera, again with two subgroups evident for genus *Pachycormus*.



PCA1, aspect ratio against pectoral fin position, *Pachycormus* is represeented in red figure '8' distribution.



PCA2, aspect ratio against fin morphotype. *Pachycormus* is represented in two red clusters, *Protosphyraean* in blue and *Bonnerichthys* in yellow..

CONCLUSIONS

The traditional descriptor of 'scythe' or 'sickle' shaped has been demonstrated to be flawed as an effective describer for pectoral fin shape in pachycormids. 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.

Reviews of characters traditionally associated with the group demonstrate that presence of rhombic scales and the 'scythe'-like pectoral fin are not pachycormid synapomorphies, and reduced ossification means that much of the skeleton in many taxa is simply not preserved. It is evident that this group requires a long overdue large-scale systematic overhaul in order to stabilise it. Thus, as our recognition of the distribution and range of both 'classic' and new pachycormid taxa worldwide has increased, so also has our need to go back and resolve the inadequate descriptions of the past, with the benefits of a much-expanded knowledge of variation in populations through the specimens that we know today.

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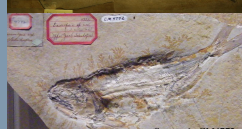
Scottish Toarcian pachycormid G1994.143.1, showing 3D preservation.

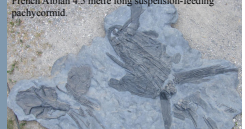

Ohmdenia, GPIT 1017


Prosauropsis, STC3


Protosphyraena – the AMNH 'Gods' Wings' specimen.


Pseudoasthenocormus, CM5399


Sauropsis, CM4772


Saurostomus NHMUK PV11126


French Albian 4.5 metre long suspension-feeding pachycormid.


Mexican Turonian suspension-feeding pachycormid


Juvenile Kimmeridgian pachycormid.

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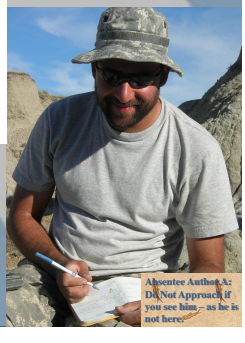
Absentee Author A: Do Not Approach if you see him – as he is not here.