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SHORT COMMUNICATION

BIOMECHANICS OF *MACHAERACANTHUS* PECTORAL FIN SPINES PROVIDE EVIDENCE FOR DISTINCTIVE SPINE FUNCTION AND LIFESTYLE AMONG EARLY CHONDRICHTHYANS

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Acanthodians are a major group of Paleozoic jawed vertebrates that constitute a paraphyletic assemblage of stem-chondrichthyans (Brazeau and Friedman, 2015). Representatives of this group are characterized, among other traits, by the presence of bony spines in front of all paired and median fins except the caudal (Denison, 1979), which has given rise to their colloquial name of ‘spiny sharks’. The occurrence of pectoral fin spines is recognized as a potential gnathostome synapomorphy (Miller et al., 2003) or symplesiomorphy (Coates, 2003), being also present in other major groups of Paleozoic jawed vertebrates, including placoderms (Young, 2010), ‘non-acanthodian’ chondrichthyans (Miller et al., 2003), and osteichthyans (Zhu et al., 1999). However, this trait was independently lost in the later evolutionary history of these lineages and is absent in most living representatives (Coates, 2003; Miller et al., 2003), with the exception of catfishes (Siluriformes), that acquired pectoral fin spines as an evolutionary reversion (Price et al., 2015). As a consequence, the paucity of living analogs precludes deriving functional interpretations of those structures and the role that they fulfilled in life remains unclear, despite this having the potential to enrich our understanding on the ecologies and lifestyles of groups of early jawed vertebrates.

Machaeracanthus constitutes a genus of acanthodians that ranged from the Late Silurian to the Middle Devonian, which is known from fin spines, scales, and a few endoskeletal remains (Burrow et al., 2010; Botella et al., 2012). The spines of this genus differ from the fin spines of all other acanthodians and sharks in presenting a marked cross-sectional asymmetry and a totally enclosed central canal, which is usually open along the proximal end of the trailing edge in other taxa (Burrow et al., 2010). The description of wear patterns at the tips of pectoral fin spines of *Machaeracanthus* and their peculiar arrangement in pairs has led some authors to propose that these elements could

have been used as ‘snow-shoes’ to lay on and prevent sinking into the substrate below or even to propel itself along the bottom (Stüdkamp and Burrow, 2007). Here, we test this hypothesis through beam theory analyses and provide evidence that the biomechanical properties of *Machaeracanthus* pectoral fin spines are compatible with this interpretation, thus shedding light on the diversity of the functions of these intriguing anatomical structures and the lifestyles of some of the earliest jawed vertebrates.

MATERIAL AND METHODS

Morphometric Analysis

The morphological diversity of *Machaeracanthus* and acanthodian pectoral fin spines was characterized by contour analysis of mid-length spine cross-sections in 21 specimens of *Machaeracanthus* corresponding to 15 different species (i.e., *M. bezieri*, *M. bohemicus*, *M. goujeti*, *M. hunsrueckianum*, *M. kayseri*, *M. longaevus*, *M. major*, *M. pectinatus*, *M. peracutus*, *M. polonicus*, *M. retusus*, *M. sarlei*, *M. sp.*, *M. sulcatus*, and *M. westfalicus*), and a representative sample of most major groups of acanthodians (i.e., one acanthodid, one climatiid, two diplacanthids, one gyracanthid, and one ischnacanthid) (Table S1). Spine cross-sectional outlines were digitized in TPS software (Rohlf, 2015) based on previously published reconstructions and figured fossil specimens in the literature (Table S1, Figs. S1 and S2 and Data S1). Elliptic Fourier analysis was then carried out in the Momocs package (Bonhomme et al., 2014) in R (R Development Core Team, 2020) considering a total number of 30 harmonics, which gather nearly 99% of the cumulative harmonic power (which is considered a measure of shape information) (Fig. S3) and reconstructs actual morphologies with high accuracy (Fig. S4). We derived a virtual morphospace by performing a principal component analysis (PCA) on the Fourier coefficients and extracted spine cross-sectional outlines corresponding to 72 equidistant coordinates (12 in PC1 x 6 in PC2) (Fig. S5), which were subsequently subjected to biomechanical analyses.

Beam Biomechanics

Beam theory has been used to study function in diverse biological structures (Therrien, 2005; Cuff and Rayfield, 2013; Murdock et al., 2013; Adams et al., 2019; Brown et al., 2020). This approach assumes that such structures behave like cantilever

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beams and predicts their resistance to bending and torsion based on their cross-sectional shape (i.e., the distribution of material around the neutral axis). Second moment of area (I) is a measure of resistance to bending in dorsoventral (I_x) and antero-posterior (I_y) directions. Resistance to torsion is measured by the polar moment of inertia (J), calculated as the sum of I_x and I_y .

We calculated I and J in three different datasets: (1) cross-sectional outlines of actual specimens, (2) cross-sectional outlines derived from the virtual morphospace (see above), and (3) serial cross-sectional outlines of two *Machaeracanthus* species (i.e., *M. bezieri* and *M. kayseri*), one climatiid, one diplacanthid, and one ischnacanthid in order to evaluate how these parameters vary along the major axis of their spines (Table S1 and Figure S6).

In all the cases, spine cross-sectional outlines were converted to binary images and imported to ImageJ v. 1.51r (Schneider et al., 2012). All the sections were considered as solid elements with no central canal, which was digitally filled in actual specimens when present. The infilling of central cavities has small impact on I and J because of its proximity to the neutral axis, as demonstrated in previous studies (Murdock et al., 2013). Sections were scaled to their original size (in actual specimens) or kept with arbitrary sizes (in virtual outlines) and I and J were calculated using the ImageJ plugin MomentMacro v. 1.4B (<https://www.hopkinsmedicine.org/faq/mmacro.html>). To remove the effect of size, I_x , I_y , and J were divided by the cross-sectional area squared, following Murdock et al. (2013).

Performance heatmaps of I_x , I_y , and J were generated with the R package ‘akima’ (Akima et al., 2016) using the data derived from the virtual outlines and plotted over the PCA morphospace to evaluate how these parameters varied with spine cross-sectional shape. We ran two-samples t-test on data derived from actual specimens to assess differences in the biomechanical properties between *Machaeracanthus* and all the other acanthodian specimens.

Finally, analyses were repeated including seven catfish (Siluriformes) specimens as living analogs (i.e., *Chiloglanis productus*, *Dianema longibarbis*, *Horabagrus brachysoma*, *Lophiobagrus cyclurus*, *Plotosus canius*, *Pseudolais pleurotaenia*, and *Schilbe mystus*) (Fig. S7 and Table S1).

RESULTS

The first principal component (PC1) is mostly related to shape changes in the roundness of the spine cross-section, increasing towards positive scores; whereas the second principal component (PC2) is mostly related to shape changes in the trailing edge, with the presence of a long lateral expansion towards negative scores and a virtually non-existent expansion or even a concave facet (i.e., representing the central canal opening) towards positive scores. *Machaeracanthus* specimens and the other acanthodians occupy distinct regions of the morphospace with no overlapping between them. The latter ones are mostly restricted to the right upper quadrant (positive PC1 and PC2 scores) while *Machaeracanthus* specimens occupy most of the remaining morphospace (Fig. 1).

Performance heatmaps derived from I_x , I_y , and J data show significant similarities, denoting that those biomechanical parameters co-vary in an important extent along the morphospace. The main change occurs roughly diagonally from the left lower quadrant (negative PC1 and PC2 scores) to the upper right quadrant (positive PC1 and PC2 scores), usually containing the highest and lowest values of I_x , I_y , and J respectively (Fig. 1). *Machaeracanthus* spines occupy regions of the morphospace that are normally associated to higher values of I_x , I_y , and J than the ones occupied by the rest of acanthodians. This is further supported by the two-samples t-tests based on results from actual specimens which find significant differences between both groups for all three biomechanical parameters

(Fig. 1). When included in the analysis, siluriform specimens fall closer to the conventional acanthodians in the morphospace and share similar biomechanical properties with them, while spines of *Machaeracanthus* species still show the highest resistance to torsion and flexion (Fig. S8).

Biomechanical analysis of serial cross-sections reveal that *M. bezieri* and *M. kayseri* show generally higher values of I_x , I_y , and J than the rest of the acanthodians in the sample at comparable positions along the major axis of the spine, but a few exceptions occur at the most proximal and distal regions. In particular, both *Machaeracanthus* specimens show lower values of I_x than the ischnacanthid and climatiid specimens at the proximal and distal ends, respectively; *M. kayseri* shows similar or slightly lower values of I_y than the ischnacanthid and diplacanthid at the distal end. The values of J in *M. kayseri* are similar to those of the ischnacanthid specimen at the proximal end and those of the ischnacanthid and diplacanthid specimens at the distal end (Fig. 1).

DISCUSSION

Our results, based on beam theory analyses, show that the cross-sectional shape of *Machaeracanthus* pectoral spines is better suited to resist dorsoventral bending (I_x), anteroposterior bending (I_x and I_y) and torsion (J) than those of ‘conventional’ acanthodians and living siluriforms. This is supported by the biomechanical performance landscape constructed from a virtual morphospace of spine cross-sections, where *Machaeracanthus* specimens usually occupy regions associated with the highest I and J . The biomechanical performance estimated for actual specimens also indicates that *Machaeracanthus* fin spines are more resistant to bending and torsion than those of other acanthodians and living siluriforms. These differences are also evident when accounting for the morphological variability along the main axis of the spine (Fig. 1).

Spines of acanthodians and other early chondrichthyans are generally presumed to have a primary function in defence and predator deterrence (Moy-Thomas, 1971; Bernacsek and Dineley, 1977; Denison, 1979; Long, 1983), but other non-mutually exclusive proposals include potential roles as cutwaters (Bryant, 1934; Johnson, 1974; Romer and Williams, 1976; Maisey, 1979; Stamberg, 2001) or as holdfasts in currents (Gregory and Raven, 1941; Westoll, 1947, 1958). The evidence presented here is compatible with a more specific function for the pectoral fin spines of *Machaeracanthus*, as structures that could provide support during bottom resting and/or assist propulsion through the substrate (Südkamp and Burrow, 2007) (see also Long, 1983; Turner et al., 2005). In these hypothetical scenarios the highest bending stress would be expected within the middle part of the spine, considering that the proximal and distal extremes of the element would be fixed to the pectoral girdle and in contact with the substrate, respectively, with the weight of the animal acting downwards (Gere and Goodno, 2012). Our results accord with this scenario, as the superior resistance to bending and torsion of *Machaeracanthus* compared to the rest of the taxa is particularly evident at the middle region of the spine (Fig. 1), denoting that cross-sectional shape variation along the spine most likely has an adaptive component in this taxon. On the other hand, the data on pectoral fin spines of ‘conventional’ acanthodians are compatible with a defensive function given the biomechanical similarity with those of living siluriforms (Wright, 2009) (Fig. S8).

Acanthodians have been classically interpreted as fishes with mostly pelagic habits, living in the middle or the surface of the water column, due to the generalized presence of fusiform bodies and well developed heterocercal tails (mostly in acanthodids, climatiids, diplacanthids, and ischnacanthids; Moy-Thomas, 1971; Denison, 1979; Janvier, 1996). However, this perspective is challenged by the recurring reports of wear facets on the spine

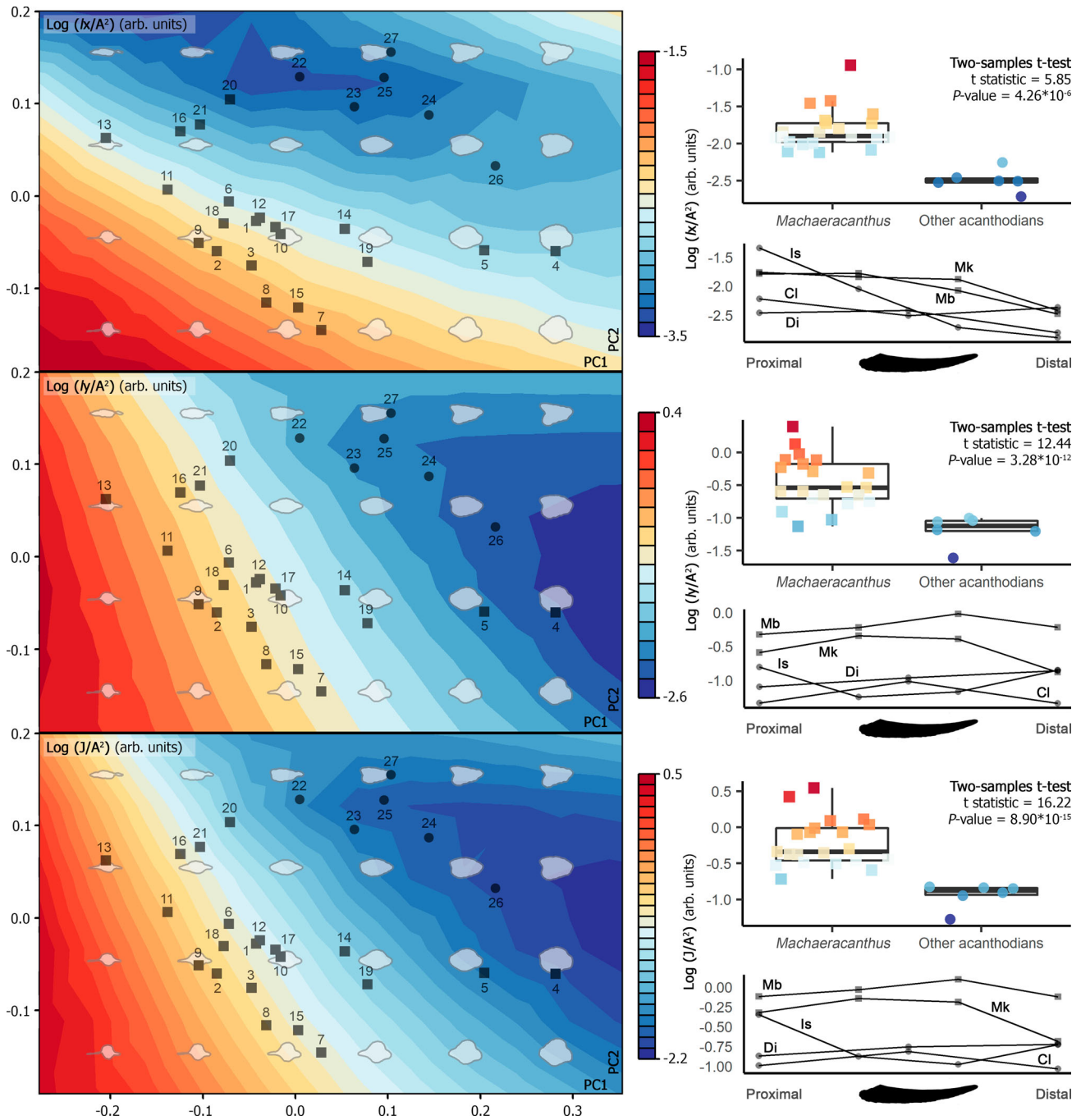


FIGURE 1. Biomechanical performance of acanthodian spine cross-sections. Left panels show performance heatmaps plotted over the obtained virtual morphospaces, representing resistance to bending in dorsoventral (I_x) and anteroposterior (I_y) directions and resistance to torsion (J) normalized by spine cross-sectional area squared (in the upper, middle, and lower thirds of the figure, respectively). Squares (*Machaeracanthus*) and circles (other acanthodians) indicate the position of actual specimens in morphospace. The right and left sides of the cross-sectional outlines correspond to the leading and trailing edge of the spine, respectively. Upper right panels show I_x , I_y , and J estimates derived from actual specimens and results of the two-samples t-test. Lower right panels show I_x , I_y , and J estimates obtained from serial cross sections along the major axis of the spine. Higher values of I_x , I_y , and J entails higher resistance to bending and torsion. 1, *M. bezier*; 2, *M. bohemicus*; 3, *M. bohemicus*; 4, *M. goujeti*; 5, *M. goujeti*; 6, *M. hunsrueckianum*; 7, *M. kayseri*; 8, *M. kayseri*; 9, *M. longaevus*; 10, *M. longaevus*; 11, *M. major*; 12, *M. pectinatus*; 13, *M. peracutus*; 14, *M. polonicus*; 15, *M. polonicus*; 16, *M. retusus*; 17, *M. sarlei*; 18, *M. sp.*; 19, *M. sulcatus*; 20, *M. westfalicus*; 21, *M. westfalicus*; 22, *Acanthodes lopatini*; 23, *Climatiidae* sp.; 24 and 25, *Diplacanthus crassissimus*; 26, “*Gyracanthus*” *sherwoodi*; 27, *Ischnacanthus gracilis*. **Abbreviations:** Cl, *Climatiid* specimen; Di, *Diplacanthid* specimen; Is, *Ischnacanthid* specimen; Mb, *Machaeracanthus bezieri*; Mk, *M. kayseri*. *Machaeracanthus* specimens are represented by squares and rest of acanthodians are represented by circles in all panels.

tips in gyracanthids (see Turner et al., 2005 and references therein) support the hypothesis that some acanthodians also swam close to the substrate (Wood and Cameron, 1998; Morrissey et al.,

support the hypothesis that some acanthodians also swam close to the substrate (Wood and Cameron, 1998; Morrissey et al.,

2004, 2006; Wisshak et al., 2004; Knaust and Minter, 2018). Our findings increase this body of evidence indicating that at least some acanthodians were adapted to a demersal lifestyle. In a broader context, this study illustrates a wider diversity of functions of acanthodian spines and suggest that there could be a functional differentiation of these anatomical structures depending on their position in the body. The unique adaptations of *Machaeracanthus* improve our understanding of the early diversification and specialization of the modes of life of the first chondrichthyans and provides new insights into the variety of lifestyles displayed by some of the earliest vertebrates with jaws.

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