We thank Britz et al. [1] for introducing Houy's [2] prescient interpretation of the significance of †Opisthomyzon for the evolution of modern remora anatomy, and regret not having discovered his elegant account ourselves [3]. Many prominent ichthyologists have considered the relevance of †Opisthomyzon since its discovery more than a century ago [4–7], but none of their observations approaches Houy’s clear explication of the sequence of evolutionary transformations associated with the origin of the adhesion disc or so closely foreshadow our own conclusions. We therefore welcome the translation provided by our co-workers and the exchange arising from their comment [1], which together give Houy the long-delayed recognition he richly deserves. However, we disagree with their claims concerning other aspects of our study.

A central theme of our co-workers’ comment [1] is that the evolutionary sequence we proposed [3] is rendered largely redundant when confronted with Houy’s [2] proposal. While we agree that our study provides corroboration for his hypothesized trajectory, it is unclear how robust phylogenetic placement of †Opisthomyzon and discovery of additional primitive features of its disc represent a duplication of past efforts. Although Houy clearly implies †Opisthomyzon is a stem remora [2], competing alignments with Phthisichthys [6,8] and Echeneis [9] that postdate his account highlight past uncertainty surrounding the affinities of this fossil. At best, these alternative placements within the remora crown render its implications for the evolution of the disc ambiguous. Recognition of past efforts is a cornerstone of science, but so too is the critical testing of old ideas using new data and techniques. Our study supports and adds to Houy’s work, because we further documented the anatomy of †Opisthomyzon and constrained its systematic position. Without a clear phylogenetic framework, †Opisthomyzon remains mute with respect to the evolution of the remora adhesion disc.

There is no doubt that the paired bones constituting the majority of the visible skull in the holotype of †Opisthomyzon are frontals. The structures labelled as parietals in this fossil [3] are depressed features at the rear of the frontals (rather than the middle of these ossifications, indicated by arrows in reference [1]) that appear to bear horn-like projections possibly representing crests. We are willing to consider an alternative interpretation as posterior extensions of the frontals, but what is agreed between previous authors [2], our co-workers [1] and us [3] is that the ornamented frontals preclude anterior extension of the disc over much of the skull in †Opisthomyzon. It is therefore surprising that our co-workers suggest that our analysis shows that the posterior position of the disc is secondary. Several factors might contribute to this confusion, and we welcome the opportunity to clarify them. Our references to ‘postcranial’ discs in both †Opisthomyzon and hypothesized sequences of character change were intended as contrasts with the extreme condition in extant remoras, where the supracranial disc extends over the entirety of the skull and terminates at the snout. We agree that some minor overlap between the adhesion disc and the hindmost skull cannot be excluded in †Opisthomyzon [1,2]. It is obvious how our terminology—meant to indicate degree of condition rather than absolutes—might be misinterpreted, and that the disc in †Opisthomyzon is more clearly described as posteriorly located. Related to this previous point, the three-state character describing fin position in
our analysis (character 88) pertains principally to the insertion of the first proximal radial. The final state does not differentiate between cases where the disc or fin extends to the anterior tip of the skull (e.g. crown-group remoras) or is largely postcranial but overlies a small portion of the rear of the skull (e.g. Coryphaena). Further characters describing the degree of cranial overlap were intentionally excluded, as they would add further weight to fin position and could be misconstrued as ‘loading the dice’ in favour of †Opisthomyzon. We could not assess the exact insertion pattern of the first proximal radial in †Opisthomyzon, and coded it as uncertain (‘?’).

This results in the optimization of an insertion anterior to pre-neural space with some cranial overlap as a synapomorphy of crown-clade Echeneoidei in the parsimony solution (optimization in the Bayesian topology is ambiguous). Significantly, and contrary to our co-workers’ assertion, this does not affect our ability to make unambiguous inferences about whether the posterior position of the disc in †Opisthomyzon represents a retained plesiomorphy or an apomorphic reversal. The extreme anterior extension of the disc in crown-group remoras is unique within Echeneoidei (figure 1a,b). All other members of Echeneoidei, as well as sampled outgroups, bear dorsal fins or discs that show minor cranial overlap or are exclusively postcranial. With this dichotomy in mind, a mapping exercise shows that it is most parsimonious to reconstruct extension of the disc to the anterior end of the skull as a unique.
innovation of crown remoras (one step; figure 1a). The shortest solution invoking a reversal in †Opisthomyzon requires two steps (figure 1b). This inference remains consistent in the face of alternative relationships within Echeneoidei [3], supporting the conclusion that many features of the disc evolved while it occupied a largely or exclusively postcranial—rather than supracranial—position [1,3].

We sympathize with the challenges of incomplete fossils alluded to by our co-workers in their comment [2] and elsewhere [11]. However, evidence does not support their claim that the lack of spinules in †Opisthomyzon represents post-mortem loss rather than genuine absence. Spinules might be removed during maceration or with forceps, but this is equally true of minute scales and fin rays that are preserved in †Opisthomyzon (figure 1c). It is unclear how these features could remain undisturbed while all spinules were removed, or how this selective process could operate identically on multiple specimens. We did consider the fossilization potential of remora spinules, which are present in ‘all other fossil representatives of the group with well-preserved adhesion discs’ [3, p. 3]. Figure 1d,e illustrates the fossil remoras referenced by this statement and described in the accounts cited in our earlier contribution [3]. These examples derive from fine-grained marine rocks (shales or mudstones) that yield abundant articulated fishes [9,12], indicating taphonomic profiles matching those of the deposits bearing †Opisthomyzon [13]. If anything, spinule preservation seems less probable for these specimens because they are more disrupted (figure 1d) or smaller and more delicate than †Opisthomyzon (figure 1c). There is another distinction between †Opisthomyzon and these fossils: they bear numerous derived features such as expanded transverse processes indicating that they branch closer to—or within—the remora crown group. Absence of spinules in fossils predicted to bear them would be troubling, but this natural control experiment illustrates clear preservation potential. Spinules evolved along the remora stem lineage, and must be lacking in some stem remoras. Attempts to explain away their absence in what is, on the basis of all available evidence, a stem remora are perplexing, and we adhere to our interpretation that the absence of spinules in †Opisthomyzon is genuine and represents a plesiomorphic condition.

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