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Mode of miniaturisation influences body shape evolution in New World anchovies (Engraulidae)

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Abstract

We explored the macroevolutionary dynamics of miniaturisation in New World anchovies by integrating a time-calibrated phylogeny, geometric morphometrics and phylogenetic comparative methods. We found that the paedomorphic species *Amazonsprattus scintilla* occupies a novel region of shape space, while the dwarf species *Anchoviella manamensis* has an overall shape consistent with other anchovies. We found that miniaturisation did not increase overall clade disparity in size or shape beyond the expectations of Brownian motion, nor were there differences in rates of size or shape evolution among clades. Overall, our study shows that while the mode of miniaturisation influences shape evolution, the phenotypic novelty produced by the evolution of miniaturisation did not seem to alter macroevolutionary dynamics.

KEYWORDS

body size, Engraulidae, geometric morphometrics, macroevolution, miniaturisation, Neotropics

1 | INTRODUCTION

The evolution of extreme body size offers insight into the limits of phenotypic evolution in animals. The patterns and processes associated with large body size are well studied and evidence for selection favouring large body size is omnipresent at both population (Roff, 1991; Stearns, 1977) and macroevolutionary scales (Albert & Johnson, 2012; Jaffe *et al*., 2011; Pimiento *et al*., 2019; Slater *et al*., 2017; Vermeij, 2012). Miniaturisation, or the extreme decrease in body size, has evolved repeatedly in animals (Hanken & Wake, 1993) and a high diversity of miniaturised fishes occur in the Neotropics (Goulding *et al*., 1988; Roberts, 1984; Steele & López-Fernández, 2014; Weitzman & Vari, 1988). However, the processes shaping the evolution of miniaturisation and the resulting phenotypic patterns are poorly known (Blackenhorn, 2000), limiting our understanding of the role of extremely small body size in diversification.

The evolution of miniaturisation can have a profound effect on phenotypic evolution and is often linked to morphological novelty (Britz *et al*., 2009; Hanken, 1986; Yeh, 2002). There are two modes of miniaturisation: paedomorphism and dwarfism. Paedomorphic species typically arise due to shifts in the developmental process (Alberch *et al*., 1979; Lovejoy, 2000) and are hypothesised to be associated with an increase in morphological variation and phenotypic novelty in a lineage (Hanken, 1986). Unlike developmentally truncated paedomorphic taxa, dwarf species resemble larger-bodied relatives (Britz *et al*., 2009; Ruber *et al*., 2007). However, the contribution of dwarf species on the phenotypic diversity of a clade is largely unknown. If dwarf species retain the same bauplan and shape dimensions as larger relatives, we predict they will reside in the same region of morphospace as non-miniaturised relatives. Under this scenario, dwarf species may not be associated with an increase in morphological variation. Alternatively, dwarf species may experience shifts that result in changes to the morphological diversity within a clade (Alberch *et al*., 1979; Britz & Conway, 2009; Britz *et al*., 2009; Buckup, 1993; Turner *et al*., 2007; Weitzman & Vari, 1988) Few studies have explored the macroevolutionary patterns and processes associated with different modes of miniaturisation nor have directly compared the effect of modes of miniaturisation on phenotypic evolution (Blackenhorn, 2000).

Miniaturisation has evolved numerous times in fishes, particularly in South American freshwater rivers (Weitzman & Vari, 1988). In this study we use New World anchovies (Engraulidae) to explore the evolution of miniaturisation. New World anchovies are divided into two major clades: the marine clade and the South American clade (Bloom & Lovejoy, 2012). The marine clade includes approximately 45 species and is dominated by near-shore, schooling and largely planktivorous species found in both the eastern Pacific and western Atlantic Oceans. The speciose genus *Anchoa* Jordan & Evermann 1927 comprises most of the species diversity in the marine clade and along with several species of *Anchoviella* Fowler 1911, tend to have superficially similar external morphology and relatedly, seem to occupy similar ecological niches. This marine clade also includes several medium-sized, deep-bodied species in the genera *Cetengraulis* Günther 1868 and *Anchovia* Jordan & Evermann 1895, as well as elongate species in the genus *Engraulis* Cuvier 1816. The South American clade, comprising six genera and more than 20 species, is ecologically diverse (Bloom & Egan, 2018; Bloom & Lovejoy, 2012; Egan *et al*., 2018a) and variable in size (Bloom *et al*., 2018). The majority of species in the South American clade are endemic to freshwater rivers in South America, but several species (*e.g*., *Lycengraulis grossidens* (Spix & Agassiz 1829) and *Lycengraulis poeyi* (Kner 1863)) are marine species that are derived from reversals back to oceanic habitats and occur along the coasts of northern South America. There are two species of miniaturised anchovies, *Amazonsprattus scintilla* Roberts 1984 (<20 mm standard length; L_S), a putatively paedomorphic species and *Anchoviella manamensis* Cervigón 1982 (<20 mm L_S), a dwarf species (Lavoué *et al*., 2010; Weitzman & Vari, 1988; Whitehead *et al*., 1988). Roberts (1984) described *A. scintilla*, the smallest clupeiform, as a paedomorphic species based on the loss or reduction of various characters, particularly the reduction of the pelvic girdle. Although the phylogenetic placement of *A. scintilla* was uncertain at the time of description, Lavoué *et al*. (2010) demonstrated that *A. scintilla* was a member of New World anchovies and Bloom and Lovejoy (2012) determined this species is a member of a clade of freshwater anchovies from South America. Cervigón (1982) described *A. manamensis* and hypothesised a phylogenetic affinity with other freshwater and estuarine members of *Anchoviella* from north-eastern South America. Several studies have clarified the phylogenetic relationships of New World anchovies and inferred the phylogenetic positions of both *A. scintilla* and *A. manamensis* (Bloom & Lovejoy, 2012, 2014; Lavoué *et al*., 2010, 2013).

In this study we investigated the patterns and processes of phenotypic evolution associated with miniaturisation. We reconstructed body-size evolution across New World anchovies to determine whether miniaturisation evolves in primarily small bodied clades, or clades with high size disparity. We examined body shape diversity across New World anchovies using geometric morphometrics to test whether the paedomorphic *Amazonsprattus scintilla* and dwarf *Anchoviella manamensis* share similar phenotypes, or whether different modes of miniaturisation occupy different regions of body shape space. Finally, we used comparative methods to explore the macroevolutionary dynamics of New World anchovies and assess whether the evolution of miniaturisation is associated with an increase in body size and body shape disparity.

2 | MATERIALS AND METHODS

No fishes were collected as part of this study, as we used specimens from a series of natural history museums. We did not perform any experiments or surgical procedures on live specimens. No part of this study involved live fishes.

2.1 | Morphometric data and analysis

We used body size data from Bloom *et al*. (2018). These authors compiled maximum L_S body size data for all Clupeiformes from Fishbase (Froese & Pauly, 2017), Whitehead *et al*. (1988) and Carpenter (2002), which we pruned to focus on New World anchovies. Standard lengths were log-transformed for subsequent analyses. For comparative analyses we used a published, multi-gene, time-calibrated phylogeny for all Clupeiformes (Bloom & Lovejoy, 2014). The original phylogeny included 52 New World anchovy species and was pruned to match our size and shape data (described below; Figure 1).

Geometric morphmetrics is ideal for quantifying shape diversity of miniaturised species because it characterises morphometric shape independent of size, location and orientation (Angielczyk & Feldman, 2013; Zelditch *et al*., 2004). Images of museum specimens of 45 species of Anchovies were taken from the left lateral side using a Nikon D750 and a 60 mm macro lens (www.nikon.com). Bent, warped, or juvenile specimens were not utilised to limit ontogenetic effects, shape distortion and other non-biological variation. Fourteen homologous, two-dimensional landmarks were used to summarise body shape using the program TPSdig 2.31 (Rohlf, 2009). The landmarks (Figure 2) included: (1) anterior end of the rostral organ (snout); (2) dorsal orbit; (3) ventral orbit; (4) posterior of supraoccipital bone of the neurocranium; (5) dorsal tip of the operculum; (6) ventral tip of the sub-operculum; (7) anterior insertion of the pectoral fins; (8) anterior insertion of pelvic fins; (9) anterior insertion of anal fin; (10) posterior insertion of anal fin; (11) posterior insertion of dorsal fin; (12) anterior insertion of dorsal fin; (13) dorsal insertion of caudal fin; (14) ventral insertion of caudal peduncle. We tested for a significant effect of size on shape using Procrustes regression with permutation (nperm = 1000) (procD.allometry function in geomorph 3.0.5; Adams *et al*., 2018). This method estimates the effect, or covariation, of centroid size with our Procrustes-aligned shape coordinates, using a linear model (Collyer *et al*., 2015).

We used a phylomorphospace approach (Sidlauskas, 2008) to investigate patterns of body shape evolution among clades and modes of miniaturisation. If miniaturised taxa evolved convergent phenotypic patterns then we expect that they would appear in proximate regions of morphospace. We predicted that dwarf taxa would only be distinguishable from larger-bodied taxa according to their body size, but not in shape space, while paedomorphic taxa would be distinguishable by both shape and size. We used the broken-stick method to inform how many principal component (PC) axes to retain for subsequent analyses. In order to visualise a morphospace for anchovy body shape, we performed a phylogenetically-explicit PC analysis (using the phyl.pca function in phytools 0.6–99; Revell, 2012) to generate a scatterplot of PC scores and then projected the phylogeny onto this morphospace using the plotGMPhyloMorphoSpace function in the geomorph package.

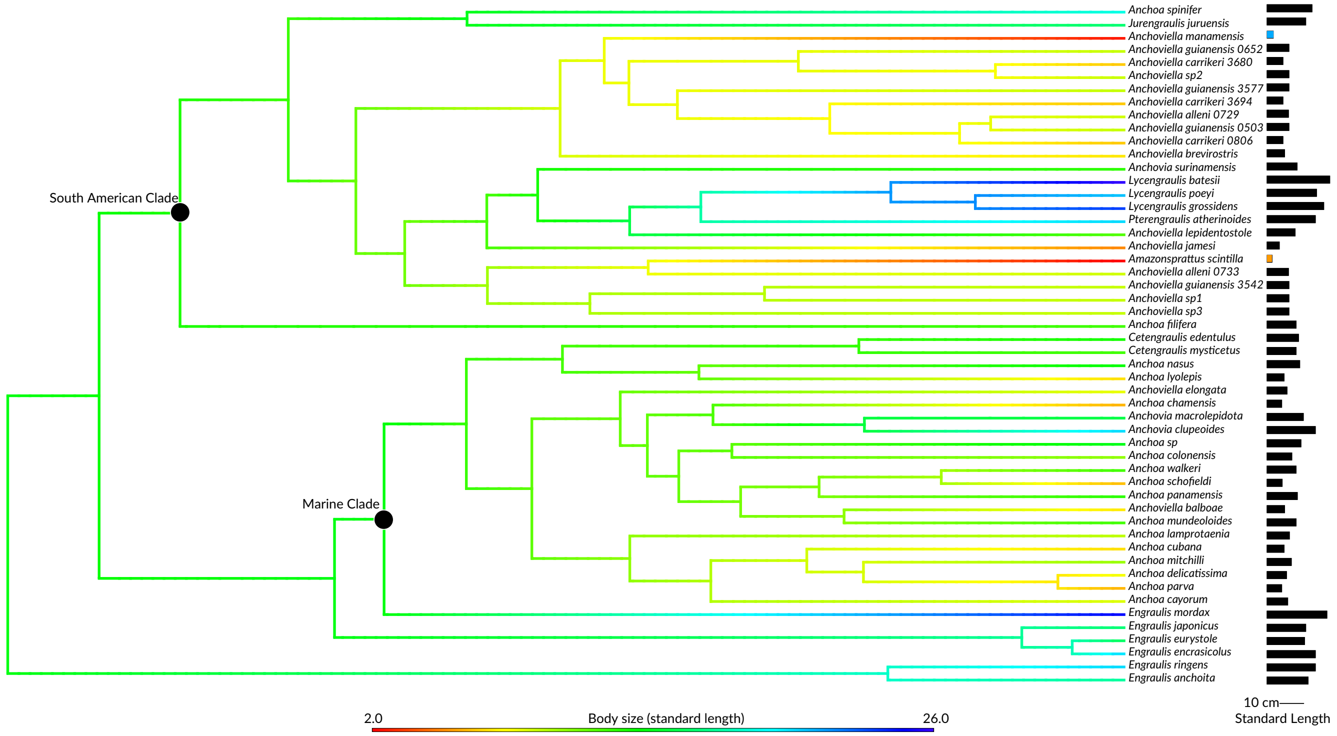

FIGURE 1 Phylogeny of New World anchovies (Engraulidae) with body size (Standard length, L_S cm) optimisd on the tree and the right panel shows L_S (■) of each species (modified from Bloom & Lovejoy, 2014)

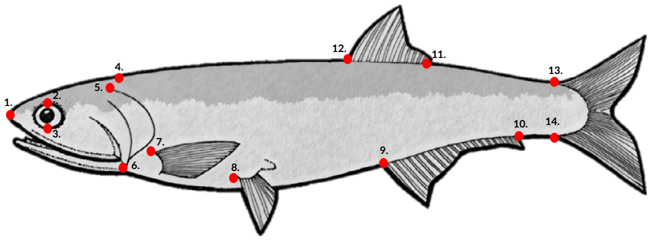

FIGURE 2 Landmarks used for geometric morphometrics of New World anchovies (Engraulidae) (●): 1, anterior end of rostral organ; 2, dorsal orbit; 3, ventral orbit; 4, posterior of supraoccipital bone of the neurocranium; 5, dorsal tip of the operculum; 6, ventral tip of sub-operculum; 7, anterior insertion of pectoral fins; 8, anterior insertion of pelvic fins; 9, anterior insertion of anal fin; 10, posterior insertion of anal fin; 11, posterior insertion of dorsal fin; 12, anterior insertion of dorsal fin; 13, dorsal insertion of caudal fin; and 14, ventral insertion of caudal peduncle

2.2 | Phylogenetic comparative methods

To explore the tempo and mode of evolution of body size and body shape evolution in New World anchovies we employed a suite of comparative analyses. First, we reconstructed body size evolution across our phylogeny using a combined stochastic character mapping and maximum likelihood node estimation approaches, using the simmap and ace functions in geiger (Pennell *et al*., 2014). We examined how trends in body size and shape disparity changed through time by calculating subclade disparity and using disparity-through-time plots (DTT) with the function ddt1 (Murrell, 2018), a modification of the dtt function in geiger (Pennell *et al*., 2014). These methods compare measured trait disparity (size or shape) relative to 10,000 Brownian motion (BM) simulations. The widely used morphological disparity index (MDI) suffers from issues with multiple testing and a high false-positive rate, so we assessed deviations from the Brownian null using the rank-envelope test (Murrell, 2018).

We were also interested in whether trends in body shape and body size traits evolved in such a way that they show either high or low phylogenetic signal. We calculated both Blomberg's *K* and Pagel's λ using phytools (Revell, 2012). Values > 1.0 for *K* suggests that trait variance is partitioned among clades, while values <1.0 suggest that trait variance is found within clades. For λ, values nearest zero suggest no correlation between species, while values nearer to one demonstrate a correlation between species that is equal to the Brownian expectation for signal.

3 | RESULTS

Our reconstruction of body size confirms that different modes of miniaturisation evolved independently in anchovies. *A. scintilla* and *A. manamensis* are members of separate clades of small-sized anchovies and both species originated early in the diversification of South American freshwater anchovies. Both miniaturised anchovy species are closely related to other relatively small-bodied species; however, the broader clade of South American anchovies includes a wide disparity of body sizes (2–300 cm).

For body shape analyses, broken-stick method estimated that the first five PC axes be retained for analysis, so these axes were used to reconstruct DTT plots and phylomorphospaces. Negative loadings on PC1 associated with elongate bodies, reduced jaw length and changes in jaw position, as well as gracile caudal regions. Conversely, deeper-bodied anchovies like *Centengraulis* Günther1868 and *Anchovia clupeoides* (Swainson 1839) loaded more positively on PC1 than other taxa, with longer jaws and taller caudal peduncles. The dwarf anchovy, *A. manamensis*, has a body shape that places it in the same region of morphospace as other members of New World anchovies, including other species of *Anchoviella* and ecologically similar species in the marine genus *Anchoa*. While *A. manamensis* only appeared distinct in body size space (Figure 3) and not in body shape space, *Amazonsprattus* was starkly delineated from other all other anchovies in both shape and size (Figure 3). The shape changes associated with the position of *A. scintilla* are a shorter jaw and smaller mouth overall, as well as truncated anal fin relative to other anchovies. While we recovered a significant effect of centroid size on body shape for all New World anchovies ($P < 0.001$), we follow the rationale of others (Evans *et al*., 2019) and did not use allometric scaling to correct our shape data, thereby retaining any biological information contained therein.

Both the South American ($P > 0.05$) and Marine clades ($P > 0.05$) showed lower disparity in log size than the Brownian expectation throughout most of their respective clade histories (Figure 4), but neither result was significant. The South American clade does not show a change in size around the stem age of miniaturised anchovies but there is an increase as the clade approaches present day. Our analysis of shape disparity through time showed that while the South American clade ($P > 0.05$) was consistent with a constant rates process, the Marine clade differed significantly from the Brownian expectation ($P < 0.01$; Figure 5). Marine anchovies consistently had higher shape disparity than the constant rates expectation, with peaks around 30 M year before present (MBP) and 10 MBP. Shape disparity in the South American clade was not significantly different from the Brownian expectation, but peaked at approximately 20 MBP, a time point that is roughly congruent with the stem ages of *Anchoviella manamensis* (18 MBP) and *Amazonsprattus scintilla* (17 MBP).

We found evidence for strong phylogenetic signal for body size using both Pagel's method ($\lambda = 0.98$, $P < 0.001$and Blomberg's K

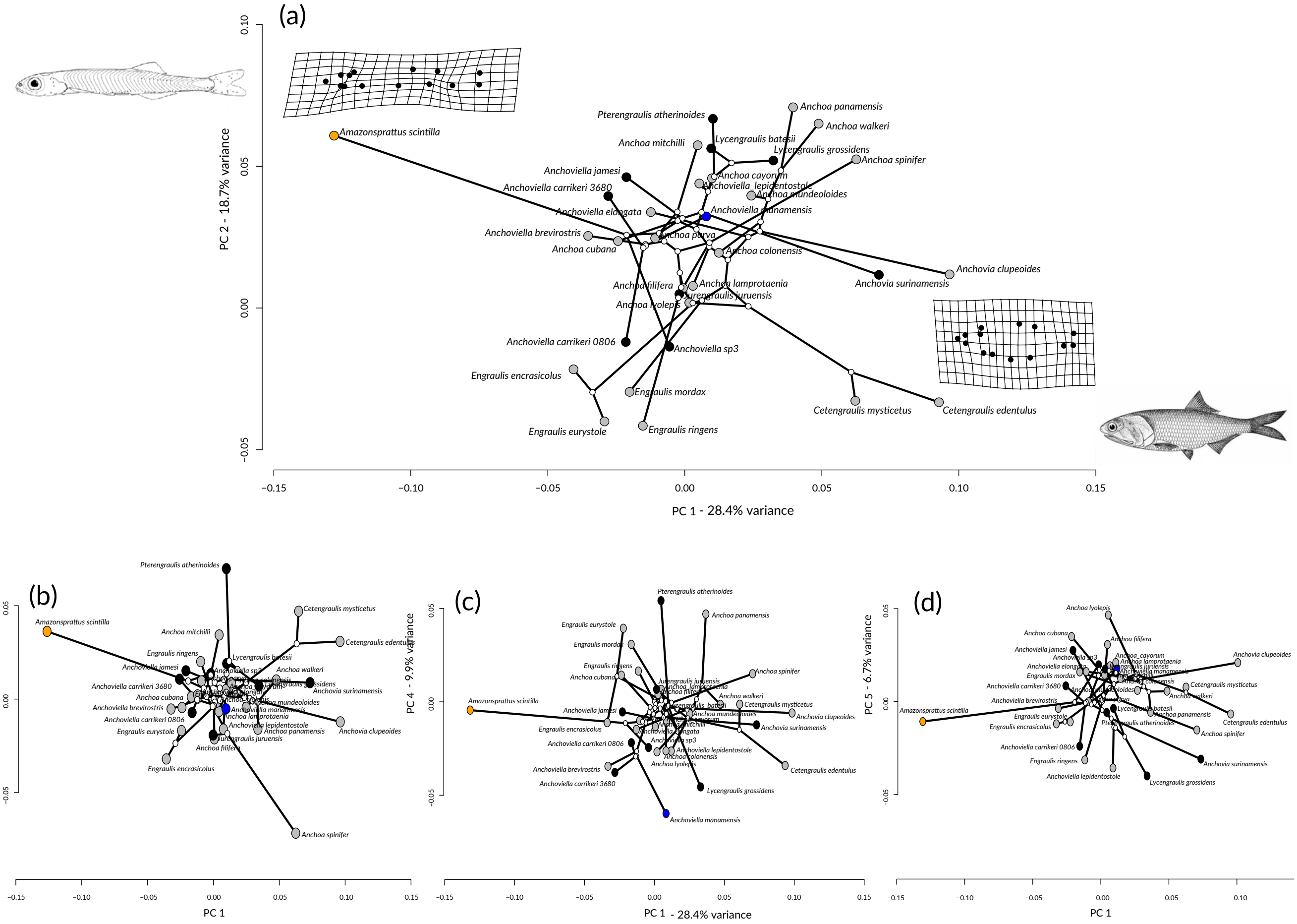

FIGURE 3 Phylomorphospace for New World anchovies (Engraulidae) generated from principal component axes from geometric morphometrics: (a) phylomorphospace based on PC1 & PC2; (b) phylomorphospace based on PC1 & PC3; (c) phylomorphospace based on PC1 & PC4; (d) phylomorphospace based on PC1 & PC5. Members of the marine clade are black, members of the South America clade are grey, *Anchoviella manamensis* is blue, and *Amazonsprattus scintilla* is orange (modified from Whitehead *et al*., 1988)

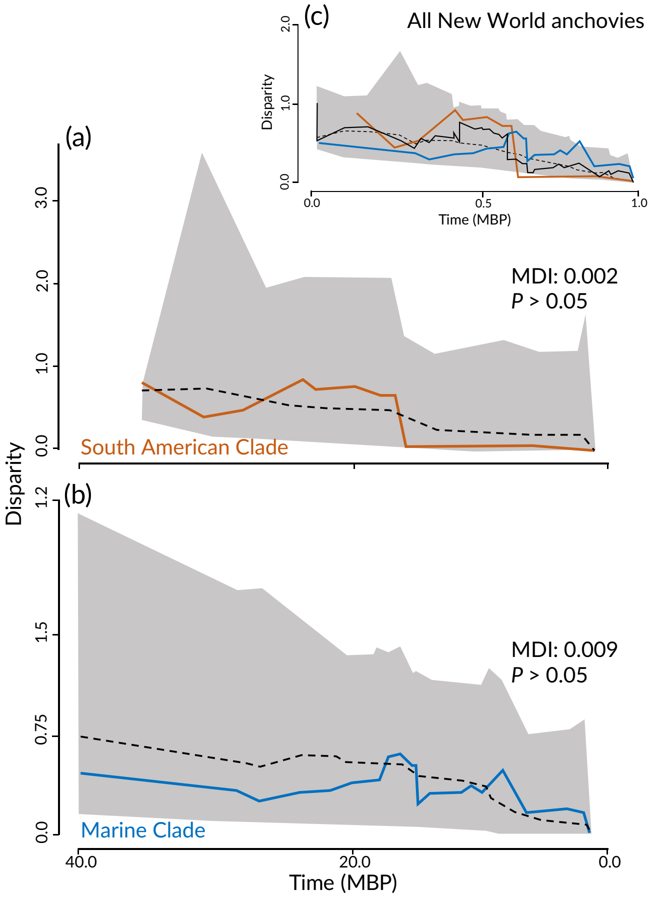

FIGURE 4 Disparity-through-time (DTT) plots of New World anchovies (Engraulidae) standard length over time for (a) the South American clade (——) and (b) the marine clade (——). (c) Comparison between these two clades and all New World anchovies. ------, Brownian simulated expectation for mean clade disparity; MBP, million years before present; MDI, morphological disparity index

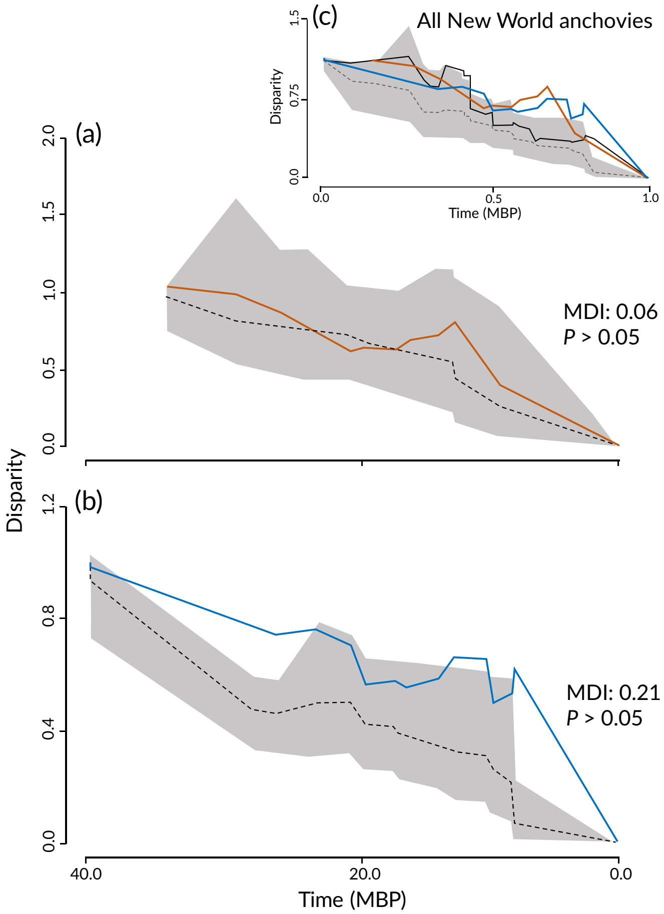

FIGURE 5 Disparity-through-time (DTT) plots of New World anchovies (Engraulidae) body shape over time for (a) the South American clade (——) and (b) the marine clade (——). (c) Comparison between these two clades and all New World anchovies. ------, Brownian simulated expectation for mean clade disparity; MBP, million years before present; MDI, morphological disparity index

(K = 0.90, $P < 0.001$). Tests of phylogenetic signal (Pagel's λ) for PC1 found that body shape is strongly predicted by the phylogeny (λ = 0.99, $P < 0.05$), corroborated by similar results using Blomberg's K (K = 0.87, $P < 0.05$). Similarly, Pagel's λ results for PC2 indicate body shape is strongly predicted by the phylogeny (λ = 0.99, $P < 0.001$); however, while Blomberg's method also shows a strong signal of the phylogeny, these results suggest that close relatives are even more similar in size than expected based on Brownian (K = 1.15, $P < 0.001$).

4 | DISCUSSION

Our analysis of body size evolution demonstrates that two distinct modes of miniaturisation, dwarfism and paedomorphism, evolved independently in South American anchovies. Miniaturisation has evolved repeatedly throughout fishes (Weitzman & Vari, 1988) and other fish clades (particularly in Otophysi) also exhibit repeated instances of miniaturisation, including both dwarfism and paedomorphism (de Santana & Crampton, 2011; Lavoué *et al*., 2008; Ruber *et al*., 2007). However, most lineages of miniaturised species are comprised entirely of either dwarf or paedomorphic species, (Frédérich *et al*., 2017; Lavoué *et al*., 2010; Takahashi & Ota, 2016), with the latter apparently the predominate mode of miniaturisation (Hanken & Wake, 1993). Both *A. scintilla* and *A. manamensis* evolved early in South American anchovies and are embedded in clades of smaller-bodied anchovies (relative to marine taxa). Phylogenetic signal for body size was strong, suggesting that miniaturisation did not necessarily involve major decreases in body size, but instead followed a continuous process of size reduction (Gould & MacFadden, 2004). Clades generally have small-sized ancestors and increase in size over their evolutionary history (Albert & Johnson, 2012; Avaria-llautureo *et al*., 2012; Guinot & Cavin, 2018). From our results for New World anchovies we infer a medium-sized ancestor that evolved both larger and smaller-bodied descendants, but the evolution of smaller extant species has been restricted to freshwater habitats.

Extreme body size is generally predicted to evolve on islands, not continents (Jaffe *et al*., 2011; Keogh *et al*., 2005; McClain *et al*., 2013; Thomas *et al*., 2009; Wollenberg *et al*., 2011). Both miniaturised species in our analysis are freshwater (continental) residents and miniaturisation evolved more commonly in freshwater environments in Clupeiformes (Lavoué *et al*., 2008; 2010; Roberts, 1972; Stiassny, 2002; Whitehead & Teugels, 1985). It is possible that certain habitats, such as riverine systems, function as island-like ecological settings (Mcclain *et al*., 2006) and offer similar ecological opportunity for extreme body size evolution. Alternatively, Thomas *et al*. (2009) argued that extreme body size is not driven by islands *per se*, but rather that when a lineage colonises an island, it is the novel environment in general that promotes phenotypic evolution. Anchovies colonised freshwater rivers of South America 20–30 MBP (Bloom & Egan, 2018; Bloom & Lovejoy, 2017; Egan *et al*., 2018a), which preceded or was synchronous with the Pebas mega-wetland (Hoorn *et al*., 2010; Wesslingh & Hoorn, 2010). The Pebas mega-wetland was a dynamic ecosystem that may have created a novel environment that set the stage for diversification of some Neotropical freshwater fishes, including freshwater anchovies (Bloom & Lovejoy, 2017). Island-like or not, new environments can drive shifts in body size evolution due to changes in competition, prey and other resource availability and associated selection on life history traits (Palkovacs, 2003; Steele & López-Fernández, 2014; Zuanon *et al*., 2006).

Extreme body size is often associated with phenotypic novelty, particularly in paedomorphic species (Britz *et al*., 2009; Hanken, 1986; Hanken & Wake, 1993; Yeh, 2002). These novel phenotypes often include the loss or pervasive reduction of traits; a remarkable example is the diminutive cyprinid *Danionella dracula* Britz, Conway & Rüber 2009 that lacks over 40 bones found in close relatives (Britz *et al*., 2009). Our results showed that the paedomorphic *A. scintilla* occupies novel body shape space for New World anchovies, supporting a general pattern of phenotypic novelty associated with this mode of miniaturisation. We also found that the dwarf *A. manamensis* has an overall body shape that is consistent with other non-miniaturised anchovies and is not associated with an increase in phenotypic disparity. Frédérich *et al*. (2017) showed that independent clades of marine dwarf angelfishes (Pomacanthidae) experienced convergent evolution and diversification into new adaptive zones. However, our results suggest that convergent body shape evolution is unlikely when lineages independently evolve extreme body size reduction *via* different modes of miniaturisation. The convergent evolution of dwarf angelfishes seems to be associated with a common shift in ecology in each respective instance, a process that may not occur when different modes of miniaturisation arise. Indeed, *A. scintilla* and *A. manamensis* are rarely collected in the same microhabitat (D.D.B., pers. obs.) and these species probably occupy different niche spaces. While the functional advantages of miniaturisation in Neotropical fishes remain unclear (Goulding *et al*., 1988), predator avoidance and competitive exclusion are possible explanations.

The presence of morphological novelty and extreme body size are factors that would seemingly prime a clade for high phenotypic disparity. However, we found no evidence that miniaturisation influences morphological disparity. Moreover, the evolution of extreme size reduction did not alter macroevolutionary processes and patterns. However, our study system includes only two origins of miniaturisation, which limits our ability to draw broad inferences on the macroevolutionary ramifications of miniaturisation. Indeed, there are cases where extreme body size has influenced macroevolutionary processes (Frédérich *et al*., 2017; Jaffe *et al*., 2011; Slater *et al*., 2017). Understanding the evolution of miniaturised Neotropical fishes will require fine-scale data on habitat occupancy, trophic niche and life history of these intriguing fishes.

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AUTHOR CONTRIBUTIONS

D.D.B. and M.K. conceived and designed the study. D.D.B., M.K., K.F. and H.W. collected the data. M.K. and K.F. analysed the data. D.D.B. wrote the first draft of the manuscript and all authors contributed to writing and preparation of the final draft.

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