



# Multilocus phylogeny, divergence times, and a major role for the benthic-to-pelagic axis in the diversification of grunts (Haemulidae)

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## ABSTRACT

We present a phylogenetic analysis with divergence time estimates, and an ecomorphological assessment of the role of the benthic-to-pelagic axis of diversification in the history of haemulid fishes. Phylogenetic analyses were performed on 97 grunt species based on sequence data collected from seven loci. Divergence time estimation indicates that Haemulidae originated during the mid Eocene (54.7–42.3 Ma) but that the major lineages were formed during the mid-Oligocene 30–25 Ma. We propose a new classification that reflects the phylogenetic history of grunts. Overall the pattern of morphological and functional diversification in grunts appears to be strongly linked with feeding ecology. Feeding traits and the first principal component of body shape strongly separate species that feed in benthic and pelagic habitats. The benthic-to-pelagic axis has been the major axis of ecomorphological diversification in this important group of tropical shoreline fishes, with about 13 transitions between feeding habitats that have had major consequences for head and body morphology.

## 1. Introduction

Haemulidae comprises a diverse group of about 145 species of percomorph fishes found throughout tropical and subtropical oceans of the world (Konchina, 1977; Nelson, 2006). Most species are marine, but some are known to enter brackish and occasionally freshwater environments (Allen and Robertson, 1994; Cervigón, 1993; Chirichigno and Cornejo, 2001; Konchina, 1977, 1976; Lindeman and Toxey, 2002; McEachran and Fechhelm, 2005; McKay, 2001; Randall et al., 1997; Thomson et al., 2000). Haemulids span diverse ecologies and body forms, from slender midwater fish to deep-bodied sand sifters, embracing a wide variety of trophic habits. Many haemulid species are opportunistic feeders that prey on a range of small, benthic invertebrates, while some others feed predominantly on zooplankton (Allen and Robertson, 1994; Cervigón, 1993; Chirichigno and Cornejo, 2001; Konchina, 1977, 1976; Lindeman and Toxey, 2002; McEachran and Fechhelm, 2005; McKay, 2001; Randall, 1967; Randall et al., 1997; Thomson et al., 2000). The daily feeding migrations of some species represent one of the most important mechanisms of connectivity between Caribbean ecosystems (Appeldoorn et al., 2009), transferring biomass, organic matter and nutrients (Helfman et al., 1982; Meyer and Schultz, 1985; Meyer et al., 1983; Shantz et al., 2015).

Haemulid phylogenetic relationships have been previously

investigated based on both morphological (Johnson, 1980; Tavera et al., 2011) and molecular grounds (Bernardi et al., 2008; Rocha et al., 2008; Sanciangco et al., 2011; Tavera et al., 2012), yet with limited taxon sampling. The monophyly of Haemulidae and its relationships with some putative allies (e.g. Lutjanidae; snappers) have been supported by morphological data, in which Haemulidae and Lutjanidae share a similar suspensorium having little direct osseous articulation and a simple symplectic (Johnson, 1980). More recently, large-scale molecular studies found haemulids inside a lutjanoid clade and usually sister to Lutjanidae (Betancur-R et al., 2013; Near et al., 2013, 2012; Wainwright et al., 2012). While previous phylogenetic studies of relationships within Haemulidae have focused on subsets of taxa, a more complete phylogeny would provide the basis for addressing a number of key questions about the history of haemulid diversification.

The benthic-limnetic axis of diversification is recognized as a major repeating theme in freshwater fish radiations where it has been described in numerous lineages (Hulsey et al., 2013; Robinson and Wilson, 1994; Schluter, 1996). Transitions between benthic and limnetic habitats have been shown to affect traits as diverse as overall body shape, fin musculature, mouth position, jaw mechanics, body coloration, and eye position (Friedman et al., 2016; Hulsey et al., 2013; Svanback and Eklov, 2004). While being better characterized in freshwater systems, a survey of marine fishes suggests a similar importance

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in several reef families (Aguilar-Medrano et al., 2011; Cooper et al., 2017; Cooper and Westneat, 2009; Floeter et al., 2017; Frédérich et al., 2013). Many radiations of marine acanthomorph fishes include some species that forage predominantly along the benthos and other species that occupy midwater habitats where they feed on fishes and smaller zooplankton. The families Lutjanidae, Sciaenidae, Sparidae, Pomacanthidae, Acanthuridae, and Lethrinidae are several examples. Haemulids also appear to show this axis of diversity but it is not known what influence foraging habitat has on haemulid body shape, feeding functional morphology or locomotor functional morphology.

Extending this issue even more generally, it is not known how locomotor and feeding functional design have been integrated during haemulid evolution. Although the functional morphology and interaction among these systems has received considerable attention in some other groups of fishes (Collar et al., 2008; Higham and Russell, 2010; Higham et al., 2007; Kane and Higham, 2011; Wainwright, 2007, 1996; Wainwright et al., 2007, 2002), it is mostly unclear the degree to which the benthic-limnetic axis is a major axis of haemulid diversification.

In this study, we used the phylogeny as a framework to ask how transitions between benthic and limnetic feeding have influenced the evolution of body shape, feeding functional morphology and locomotor functional morphology in haemulids of the New World. We enumerate benthic/limnetic transitions and compare the morphology and body shape of haemulids that feed in these two habitats.

## 2. Material and methods

Specimens were obtained through field collections around the Caribbean, Eastern Pacific, and Indo-Pacific (Table S1). Preserved specimens were stored and examined at the Mexican fish collections of Centro Interdisciplinario de Ciencias Marinas, and Centro de Investigaciones Biológicas del Noroeste. Additional taxa were measured and photographed at the California Academy of Sciences.

### 2.1. Phylogenetic analysis

The phylogeny presented here is a subset pruned from a larger phylogeny of 147 taxa (Fig. S1) built to allow the inclusion of non-haemulid fossil calibrations. This phylogeny was constructed from a combination of newly generated DNA sequences and data available on GenBank. Most of the new data (Table S1) belongs to haemulid species that have not been previously included in any phylogenetic study of this family (Sanciangco et al., 2011; Tavera et al., 2012).

We used all loci (COI, Cytb, 16S, RAG2, S7) and taxa from Tavera et al. (2012), to which we added 34 species and two additional nuclear genes (RAG1 and TMO 4c4). Qiagen DNeasy Blood and Tissue kits were used to isolate DNA from tissue samples. Previously used PCR primers, reactions and programs can be found in Tavera et al. (2012). RAG1 and TMO, primers, reactions and programs used where those outlined in Lopez et al. (2004) and Streelman et al. (1998).

The seven gene fragments were aligned using the MAFFT algorithm in Geneious. The combined dataset contained 4,144 bp. Seventeen data partitions were designated corresponding to codon positions of protein coding genes and two for the non-coding positions. jModeltest 2.1.1 (Posada, 2008), was used to independently evaluate the substitution models of each partition, and the corrected Aikake Information Criterion was used to select among the options. A partitioned Maximum Likelihood run was performed in RAxML 7.2.6 (Stamatakis, 2006), under the GTR + G substitution model. The resulting tree was used as the starting option for the divergence time analysis.

### 2.2. Time calibration

To estimate divergence times, we first tested for and rejected a strict molecular clock. An uncorrelated lognormal relaxed clock prior was selected as the model of evolutionary rate, and implemented in the

phylogenetic reconstruction in BEAST v1.8.1 (Drummond and Rambaut, 2007; Heled and Drummond, 2012). The dataset was partitioned unlinking the nucleotide substitution models among the codon-based partitions, and the UCLN clock model among the genes. The birth-death process was chosen as the tree prior. Three independent fossil dates were taken from previous studies (Near et al., 2013, 2012) and used to time-calibrate our phylogeny. The calibrations used included a stem lineage Siganidae, dating the MRCA of *Siganus* and *Scatophagus* (*Scatophagus* and *Selenotoca*); a stem lineage Acanthurinae, dating the MRCA of *Acanthurus* and *Naso*; and a stem lineage Luvaridae, dating the MRCA of *Luvarus*, *Zanclus*, and Acanthuridae. For additional information on fossils dates see (Near et al., 2013, 2012).

BEAST analyses were run three times. The number of generations varied depending on mixing and convergence of chains. All parameters were sampled every 1000 generations. Mixing and convergence statistics were monitored in Tracer v1.5. Runs were combined in LogCombiner v1.8.1, and TreeAnnotator v1.8.1 was used to generate the maximum clade credibility tree from the resulting trees after discarding the first 25% of sampled trees as part of the burn-in phase.

### 2.3. Functional and morphological diversification

We explored the morphological diversity of New World haemulids, a monophyletic group for which we had specimens from more than 95% of all valid extant species. We built a set of functional traits associated with locomotion, a set of functional traits associated with feeding, and a landmark morphometric data set for lateral-view body shape. Thirteen functional traits were chosen from previous studies that showed them to be associated with fish feeding and swimming performance in other acanthomorph fishes (Carroll et al., 2004; Price et al., 2013; Wainwright et al., 2007). Locomotion traits included caudal surface area, caudal fin aspect ratio and caudal fin depth factor, all measurements of size and shape of this propulsive surface (Fisher and Hogan, 2007; Webb, 1984). Body fineness ratio was calculated as fish standard length divided by the square root of maximum body depth times maximum body width. Fineness ratio for fish bodies, when considered independent of body size, is expected to be negatively correlated with drag (Bainbridge, 1960). We also measured maximum body depth position as a fraction of fish standard length, and pectoral fin height, which has a role in stability during braking (Higham, 2007), as a fraction of body depth.

Feeding traits included maximum mouth gape, measured laterally between the medial surfaces of the coronoid process of the dentary when specimens had mouth completely open, length of ascending process of the premaxilla which is an indication of the amount of jaw protrusion, length of longest gill raker on the first gill arch, and mass of the jaw-closing adductor mandibulae muscle (AM mass). In addition, we calculated mechanical advantage of jaw closing (close ratio) as the ratio between the distance between the articular-quadrate jaw joint and the attachment of the adductor muscle on the mandible divided by the distance between the jaw joint and the anterior margin of dentary teeth. The jaw opening ratio (open ratio) was calculated as the distance from the jaw joint to the attachment of the interopercular-mandibular ligament divided by the distance between the jaw joint and the anterior tooth row of the dentary. Finally, we calculated suction index, a morphologically based estimate of the capacity to generate suction pressure during prey capture (Carroll et al., 2004; Collar and Wainwright, 2006; Wainwright et al., 2007).

All linear measurements were log transformed while we took the square root of areas and cube root of masses prior to log transformation. Subsequently we did a phylogenetic size correction and to reduce dimensionality we performed a phylogenetic PCA (Revell, 2009) with each data set independently. The broken stick method was used to determine the number of principal components that were retained. All dataset manipulations and statistics were performed in R using the Ape (Paradis et al., 2004), Geiger (Harmon et al., 2008), and Phytools

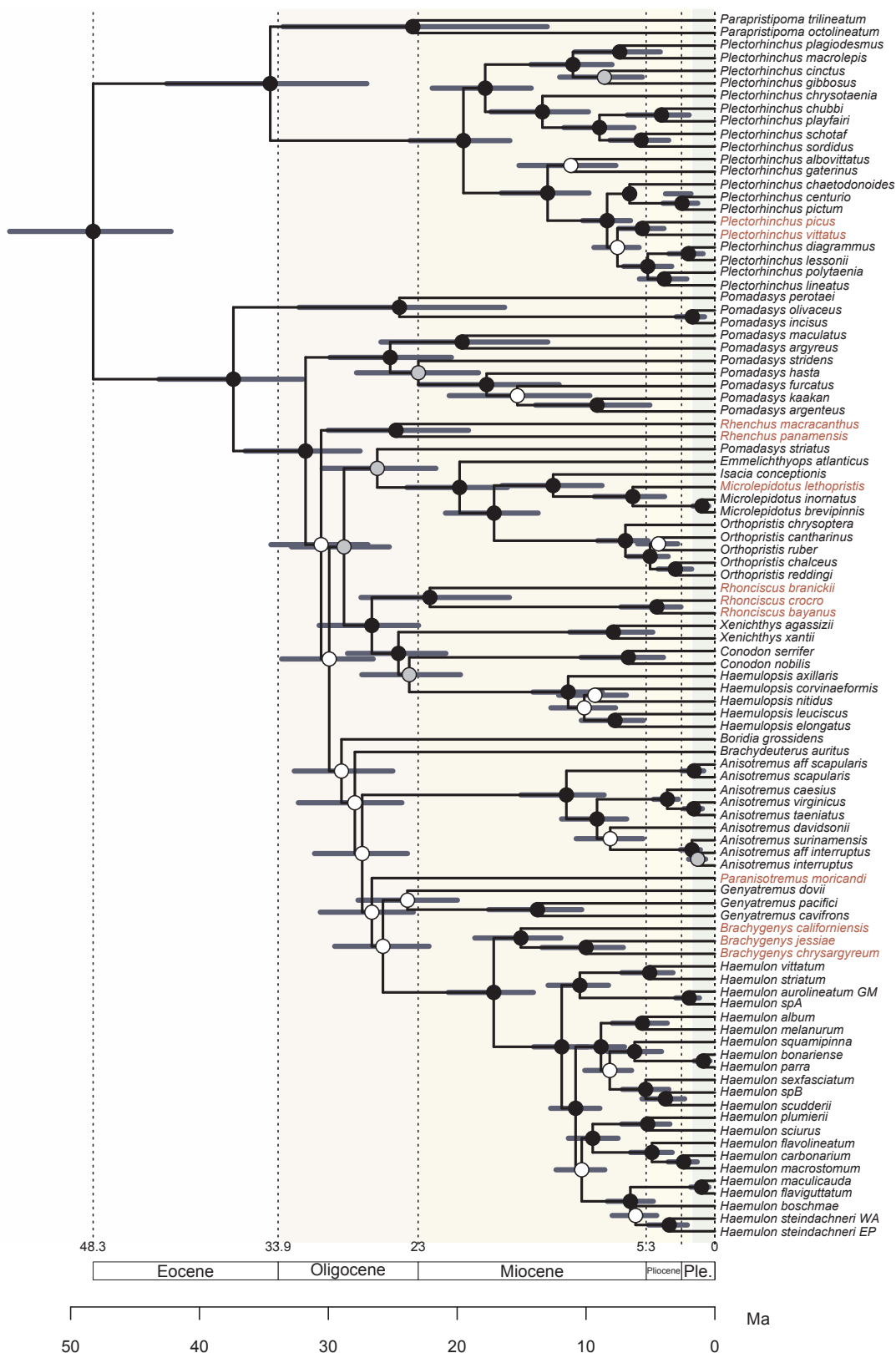


Fig. 1. BEAST maximum clade credibility tree of the family Haemulidae. Black circles on nodes correspond to a support value of 1 posterior probability (pp). Gray circles correspond to 0.75–0.95 pp. White circles indicate 0.75 pp or below. Blue bars correspond to 95 CI of estimated age for each node. Species in red are those in which a new taxonomic allocation is proposed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Revell, 2012) phylogenetic packages.

Body shape was quantified using geometric morphometrics. 23 anatomical landmarks and 13 semilandmarks (see Fig. S2 for a

photograph indicating location of these landmarks) were selected and digitized on lateral-view photographs of each specimen. The semi-landmarks were used to describe head profile and lateral line contour.

**Table 1**  
Major taxonomic amendments to actual classification, including current name and proposed change.

Current taxonomic allocation	Proposed taxonomic amendment
<i>Diagramma centurio</i>	<i>Plectorhinchus centurio</i>
<i>Diagramma pictum</i>	<i>Plectorhinchus pictum</i>
<i>Anisotremus moricandi</i>	<i>Paranisotremus moricandi</i>
<i>Haemulon chrysargyreum</i>	<i>Brachygenys chrysargyreum</i>
<i>Xenistius californiensis</i>	<i>Brachygenys californiensis</i>
<i>Xenocys jessiae</i>	<i>Brachygenys jessiae</i>
<i>Orthopristis lethopristis</i>	<i>Microlepidotus lethopristis</i>
<i>Pomadasy bayanus</i>	<i>Rhonciscus bayanus</i>
<i>Pomadasy branickii</i>	<i>Rhonciscus branickii</i>
<i>Pomadasy crocro</i>	<i>Rhonciscus crocro</i>
<i>Pomadasy macracanthus</i>	<i>Rhencus macracanthus</i>
<i>Pomadasy panamensis</i>	<i>Rhencus panamensis</i>

The former is related to mouth position and suction feeding performance (Carroll et al., 2004; Higham et al., 2006) and the lateral line functions in the detection of pressure differentials and may be particularly significant in this group of largely nocturnal fishes (Bleckmann, 1993, 1994; Montgomery et al., 1997; Bleckmann and Zelick, 2009). Landmark data were taken from photographs of at least three (up to five) adult individuals per species. Photographs of 397 individuals from 96 haemulid species were used. Semilandmarks were used to represent homologous curves by sets of points, establishing a geometric homology. We selected 20 and 40 points for each curve (head profile and lateral line, respectively), distributing them equidistantly using TPSDig 2.1.2. We then slid them along the curve minimizing bending energy between individuals and the Procrustes mean shape (Gunz and Mitteroecker, 2013). Afterwards they were reduced to five and eight semilandmarks respectively, that encompass most of the variation in these curves. After the sliding process, landmarks and semilandmarks were treated the same way in subsequent statistical analyses. Landmark configurations for each specimen were aligned using a generalized Procrustes superimposition and averaged species shapes were obtained using the Geomorph library (Adams and Otárola-Castillo, 2013) in R (R Core Team, 2007). TPSrelw v1.5.1 was used to perform a partial warp analysis. Finally, a matrix of scores of all species in each of the partial warps was generated and subjected to a phylogenetic PCA (Revell, 2009).

To label species by feeding type we gathered published data on the most common location that each species was found in the water column when it feeds (Allen and Robertson, 1994; Cervigón, 1993; Chirichigno and Cornejo, 2001; Grove and Lavenberg, 1997; Hobson, 1965; Hobson and Chess, 1976; Konchina, 1977, 1976; Lindeman and Toxey, 2002; McEachran and Fechhelm, 2005; McKay, 2001; Randall et al., 1997; Thomson et al., 2000). Species qualified as benthic feeders if they fed only, or mostly, on benthic prey (e.g. sediment-dwelling invertebrates), while pelagic feeders refers to species that consume mostly mobile mid-water prey (e.g. zooplankton, small fishes). By means of phylogenetic MANOVAs and ANOVAs we asked whether morphology of feeding, locomotion and body shape differed in benthic and midwater feeders, using principal component scores and independent traits, respectively. We also explored how feeding regime affected morphospace occupation of species using convex hulls in R using APE (Paradis et al., 2004), Geiger (Harmon et al., 2008), and Phytools (Revell, 2012) phylogenetic packages.

To test whether locomotion traits, feeding traits, and body shape are correlated we tested for correlations between all principal axes of phenotypic variation in each data set by means of multivariate phylogenetic generalized least squares (PGLS) using feeding type as a co-factor. These analyses were conducted in R using the geomorph and nlme libraries (Adams, 2014; Pinheiro et al., 2015). To account for phylogenetic uncertainty, we ran all the analyses on a random set of 1000 trees sampled from the posterior distribution of trees obtained after a 25% burn-in of the combined set of BEAST runs.

## 2.4. Ancestral habitat reconstruction

To infer the history of transitions between benthic and pelagic feeding, we used Bayesian stochastic character mapping of this two-state trait (Huelsenbeck et al., 2003) implemented in SIMMAP (Bollback, 2006) in R (R Core Team, 2007), through the Phytools package (Revell, 2012). We tested two possible models (i.e. equal rates “ER” and all rates different “ARD”) and compared them using a likelihood ratio test. We ran the SIMMAP analysis using the model that best fit our data on both a single MCC tree from our BEAST analysis, as well as a subset of 500 random trees from the post-burn-in posterior distribution. For each of the trees in this subset of post burn-in trees, 200 simmaps were done to help account for uncertainty in the divergence-times and phylogenetic topology. However, posterior probabilities for ancestral nodes were not used because different trees in the posterior sample have different nodes and node numbers. In order to estimate a specific history of feeding habitat, 10,000 SIMMAPs were made on a single MCC tree and posterior probabilities for all nodes were summarized and presented on this topology.

## 3. Results

Phylogenetic analyses on the concatenated set of genes revealed taxonomic inconsistencies as highlighted in Fig. 1. Monophyly of both Haemulinae and Plectorhinchinae was supported by posterior probabilities of 1 and bootstrapping of 100%. Within the Plectorhinchinae the paraphyly of *Plectorhinchus* (*Diagramma* nested inside) was strongly supported (Fig. 1). Among Haemulinae *Pomadasy* was rendered polyphyletic and split into at least four widely spread groups. *Orthopristis lethopristis* was recovered sister to *Microlepidotus* instead of the remaining members of *Orthopristis*. And *Anisotremus moricandi* was ambiguously placed between *Anisotremus* (sensu Tavera et al., 2011) and *Haemulon* + *Xenocys* + *Xenistius* (Fig. 1). Given these taxonomic conflicts a new taxonomic arrangement is proposed and summarized in Table 1 and Fig. 2. Some relationships among Haemulidae genera, particularly within Haemulinae, were not fully resolved, and may be challenging to recover given the apparently rapid radiation of these clades; though there is strong support for most of them (Fig. 2).

The BEAST analysis reached convergence according to monitored ESS parameters in Tracer v.1.5. The Bayesian analysis resulted in a well-resolved phylogeny with high support values for many of the backbone nodes (Fig. 1). Nine well-resolved major clades were found: (1) *Parapristipoma*; (2) *Plectorhinchus* + *Diagramma*; (3) *Pomadasy* group 1 (*P. perotaei* + (*P. olivaceus* + *P. incisus*)); (4) *Pomadasy* group 2 ((*P. maculatus* + *P. argyreus*)) + (*P. stridens* + (*P. hasta* + (*P. furcatus* + (*P. kaakan* + *P. argenteus*))))); (5) *Pomadasy* group 3 (*P. macracanthus* + *P. panamensis*); (6) *Emmelichthypops* + *Isacia* + *Microlepidotus* + *Orthopristis*; (7) *Pomadasy* group 4 (*P. branickii* + (*P. crocro* + *P. bayanus*)) + *Xenichthys* + *Conodon* + *Haemulopsis*; (8) *Anisotremus* (sensu Tavera et al., 2011); and (9) *Xenistius* + *Xenocys* + *Haemulon*. Two additional valid monotypic genera, *Boridia* and *Brachydeuterus*, as well as the species *Anisotremus moricandi*, were ambiguously placed in the tree.

The molecular clock model was rejected for all seven gene regions and the UCLN relaxed- clock model was used. Our dated phylogeny (Fig. 1) estimates a 95% confidence interval of 54.7–42.2 Ma, with a mean value of 48.3 Ma, for the initial split of Haemulinae and Plectorhinchinae which are nearly geographically isolated today. The crown age of Plectorhinchinae (*Plectorhinchus* (including *Diagramma*) + *Parapristipoma*) was estimated to be around 34.5 Ma (95% HPD: 42.6–27 Ma), whereas Haemulinae appears to be slightly older at 37.4 Ma (95% HPD: 43.2–32 Ma). The crown age of Haemulinae (includes all New World species) spanned from 36.5 to 27.5 Ma with a mean value of 31.8 Ma.

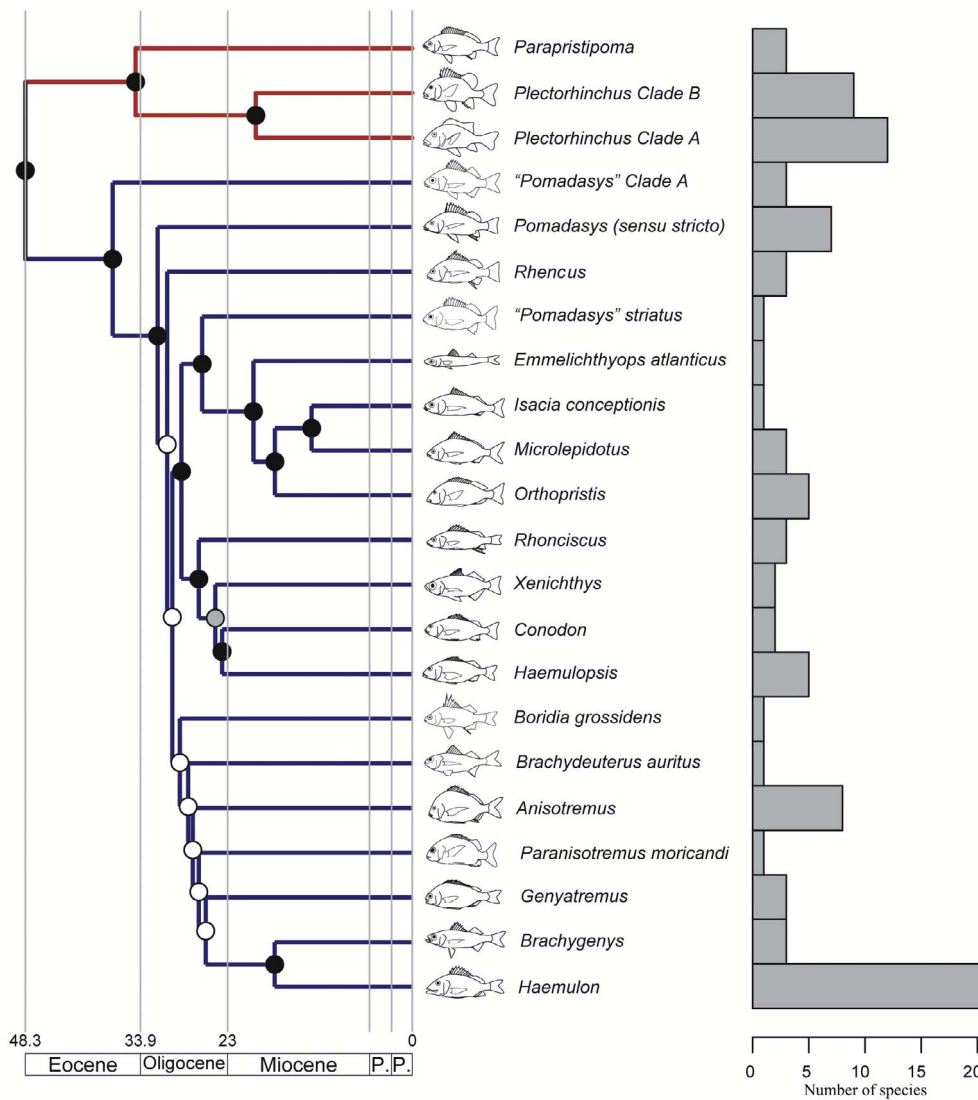


Fig. 2. Cartoon tree summarizing new generic phylogenetic classification. Blue line indicates subfamily Hamulinae and red Plectorhinchinae. Gray bars in the right of the figure corresponds to species richness in each genus. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

### 3.1. Functional and morphological diversification

The first three PC axes are summarized in Tables 2 and 3 for both feeding and locomotion traits. Gape width and lower jaw opening mechanical advantage had the highest loadings on trophic PC1, that accounts for 36% of total variance. Premaxilla ascending process length loaded heavily in the second trophic PC, which accounted for about 27% of total variance (Table 2). In the locomotion trait PCA caudal peduncle area and pectoral fin height loaded highest on PC1 (37%) while caudal peduncle depth factor and caudal aspect ratio loaded highest but in opposite directions on PC2 (Table 3).

**Table 2**  
Loadings from phylogenetic principal components analysis of feeding traits with variance explained by the first three PCs.

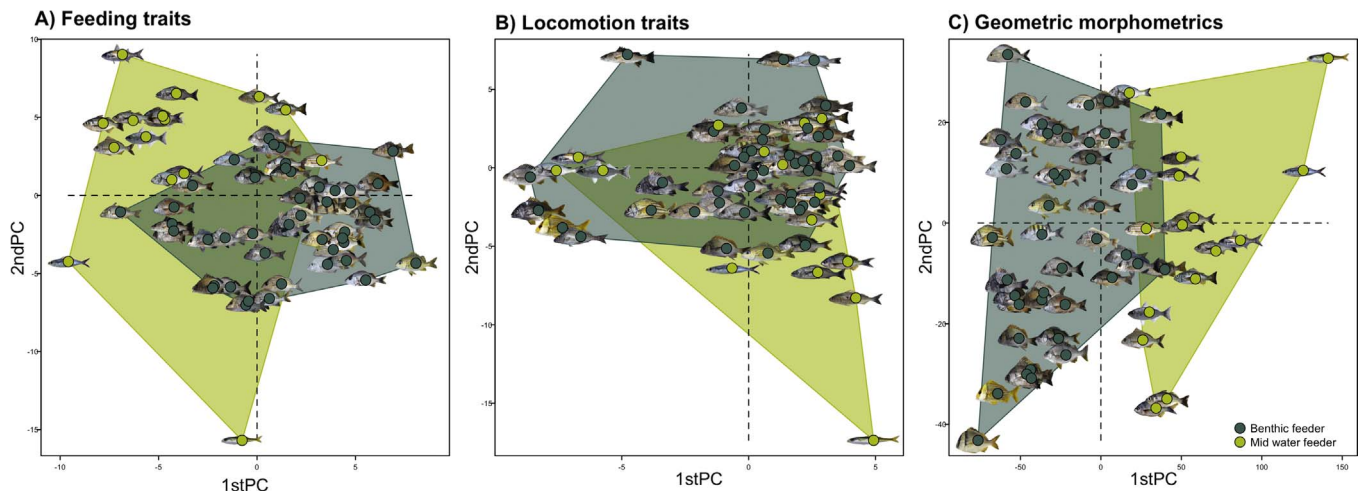
Trait	PC1	PC2	PC3
Gape width	0.94	−0.03	−0.08
Ascending process length	0.26	−0.74	0.39
Adductor mandibulae muscle mass	0.29	−0.58	0.61
Longest gill raker length	−0.39	0.66	0.55
Suction index	−0.62	−0.48	−0.22
Lower jaw open ratio	0.83	0.04	−0.36
Lower jaw close ratio	0.52	0.56	0.35
Explained variance (%)	36.2	26.8	16.2

The major axis of body shape variation (41% of the total variance) among New World haemulids contrasted deep-bodied species with more slender-bodied, elongate forms (Fig. 3C). Principal component 1 describes the difference between deep (high scores) and slender bodies (low scores). PC2 (15.6% of total variance) captures change in the length of the spiny portion of the dorsal fin, and length of the snout. Species with high scores on this axis have longer spiny dorsal fin and shorter snouts.

In all three data sets there is a trend toward a difference in average morphology of species that forage in benthic versus midwater habitats, particularly with overall body shape (Fig. 3). Species that forage in midwater have slenderer, elongate bodies and benthic feeders are

**Table 3**  
Loadings from locomotion phylogenetic principal components analysis and variance explained.

Traits	PC1	PC2	PC3
Max body depth position/standard length	−0.77	0.06	−0.04
Fineness ratio	0.21	−0.28	−0.9
Caudal peduncle depth factor	−0.156	0.87	−0.07
Caudal peduncle area	−0.83	0.17	0.04
Caudal aspect ratio	−0.38	−0.68	0.36
Pectoral fin height	0.84	0.15	0.38
Explained variance (%)	37	22.6	18.2



**Fig. 3.** Morphological principal component analyses of New World grunts. (A) Feeding morphospace. (B) Locomotion morphospace. (C) Shape morphospace measured by geometric morphometrics. Colored polygons represent distinct ecological habits. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 4**

Results from phylogenetic MANOVAs testing for differences in morphology between mid–water and benthic feeding regimes for the two functional trait data sets and morphometric body shape.

Traits	Wilks lambda	df	p
Feeding	0.4113511	52	0.000999
Locomotion	0.4975061	53	0.002997
Shape	0.0175238	9	0.012987

**Table 5**

Results from phylogenetic ANOVAs testing for differences in average feeding functional morphology between mid-water and benthic feeding regimes.

Traits	F	p
Gape width	18.99	0.002
Premaxilla ascending process	11.16	0.010
Adductor mandibulae mass	9.545	0.032
Gill raker length	8.76	0.044
Suction index	7.95	0.049
Lower jaw opening mechanical advantage	23.38	0.002
Lower jaw closing mechanical advantage	4.76	0.111

**Table 6**

Results from phylogenetic ANOVAs testing for differences in average locomotion functional morphology between mid-water and benthic feeding regimes.

Traits	F	P
Max body depth position/standard length	1.338	0.411
Finness ratio	40.482	0.001
Caudal peduncle depth factor	0.002	0.977
Caudal peduncle area	2.743	0.208
Caudal aspect ratio	0.791	0.531
Pectoral fin height	15.124	0.002

deeper-bodied (Fig. 3C). Phylogenetic MANOVAs revealed a significant effect of feeding habitat on all included data sets (Table 4). Separate phylogenetic ANOVAs on each trait for feeding and locomotion data are reported in Tables 5 and 6.

All regression models describing multivariate shape using functional traits as predictors and feeding type as cofactor were statistically significant (Table 7; Fig. 4a). PGLS regressions were made on 1000 random BEAST phylogenetic trees giving significant p values for every iteration. Regression trajectories differed among feeding types for both the full model in which we included feeding and locomotion traits as

predictors of shape as well as for the locomotion and feeding correlation (Table 7).

### 3.2. Ancestral habitat reconstruction

Both likelihood ratio test ( $P = 0.1902374$ ) and delta AICC ( $\delta = 0.3716458$ ) indicate no support for the more complex model ARD over a simpler ER, therefore the latter was chosen. The SIMMAP reconstructions revealed between 5 and 19 transitions between feeding habitats with an overall average of 13.4 transitions. The most common state across Haemulidae was benthic feeding, with the SIMMAP reconstructions spending 0.84 of the time in this state. Most transitions were from benthic to pelagic feeding mode (mean 11.1 transitions per simulation), while pelagic to benthic transitions were far less common (mean 2.3 transitions per simulation). Further, most of the inferred changes from pelagic to benthic feeding occurred within long branches and ended up as reversals into benthic feeding at the tip, except for the possible reversal to benthic feeding in the “*Orthopristis*” clade (Fig. 5). Two different scenarios for the evolution of pelagic feeding species can be inferred for the latter; (i) a benthic-to-pelagic transition occurred on the branch leading to the clade containing *Emmelichthys*, *Isacia*, *Orthopristis*, and *Microlepidotus*, followed by a pelagic to benthic reversal in the ancestor of *Orthopristis* (excluding *O. lethopristis*); or (ii) two independent benthic to pelagic transitions occurred, one in the ancestor of the *Isacia* + “*Orthopristis*” *lethopristis* + *Microlepidotus* clade and the other in *Emmelichthys atlanticus*. The latter scenario seems to me more probable as it occurred most frequently in our simulations, as can be seen in the marginal ancestral states (Fig. 5). Haemulidae was reconstructed to have been a benthic feeder in its ancestral state. Transitions between benthic and pelagic feeding modes occurred throughout the history of Haemulidae, although the rate of transition per unit of branch length peaked between 35 and 15 Ma (Fig. 4).

## 4. Discussion

Our phylogenetic analysis includes about 45% more Haemulidae species (97 spp) than presented previously (Sanciagco et al., 2011, 56 spp; Tavera et al., 2012, 54 spp). While our analyses generally support previous results, there are also some novel findings. We resolve Haemulidae into nine highly supported (BPP = 1) subclades, some of them including more than one genus (Fig. 1). The phylogenetic resolution of this study, plus the high support for many clades, allows us to revise grunt classification in a phylogenetic context and provide a new, comprehensive taxonomy (Table 1).

**Table 7**

Results from PGLS statistical analyses of different components of grunts morphology, including shape and locomotion and functional morphology between mid-water and benthic feeding regimes.

Full model <sup>a</sup>	SS	MS	R <sup>2</sup>	df	F	P
Feeding	4584.2	654.89	0.235	7	6.139	0.001
Locomotion	8125.5	1354.25	0.4169	6	12.694	0.001
Feeding type	317.1	317.07	0.0163	1	2.972	0.001
Feeding × feeding type	1324.4	189.2	0.0679	7	1.774	0.001
Locomotion × feeding type	1725.4	287.57	0.0885	6	2.696	0.001
Feeding ~ locomotion × feeding type	SS	MS	R <sup>2</sup>	df	F	P
Locomotion	108.94	18.156	0.2637	6	5.7959	0.037
Feeding type	86.99	86.987	0.2106	1	27.767	0.001
Locomotion × feeding type	72.98	12.163	0.1767	6	3.8829	0.001

<sup>a</sup> Full model: Shape ~ Feeding + Locomotion + Feeding × Feeding type + Locomotion × Feeding type.

At the base of Haemulidae we found strong support for monophyly of both Plectorhinchinae and Haemulinae and their status as sister groups. This result is consistent with previous morphological (Johnson, 1980) and molecular studies (Liang et al., 2012; Sanciangco et al., 2011; Tavera et al., 2012).

Based on morphology, three genera have been traditionally recognized in Plectorhinchinae: *Diagramma*, *Parapristipoma*, and *Plectorhinchus* (Konchina, 1976; Nelson, 2006, 199, 1984, 1976). However, our analyses, as well as others (Sanciangco et al., 2011; Tavera et al., 2012), place *Diagramma*, including type species *D. pictum* (Thunberg 1792), deeply nested within *Plectorhinchus*, sister to its type species *P. chaetodonoides* Lacepède 1801, implying that this genus (*Diagramma* Oken 1817) should be considered a synonym of *Plectorhinchus* Lacepède 1801. Therefore, the valid genera in Plectorhinchinae must be reduced to *Plectorhinchus* and *Parapristipoma*, both of which are strongly supported in our analyses (posterior probability of 1).

With 19 out of 28 valid species of *Plectorhinchus* included in our study, our phylogenetic hypothesis supports two subclades, each displaying distinctive morphological, ecological and coloration features. Species in subclade A mostly have deeper body shapes, and tend to be uniformly dull-colored compared to those in subclade B (Figs. 1 and 2), which are generally coral reef-associated with a significant preference for inhabiting water with good visibility, such as in lagoons and seaward reefs (Johnson et al., 2001; Lipej et al., 1996; McKay, 2001; Moazzam et al., 2006; Randall et al., 1997).

We resolve Haemulinae into twelve highly supported polytypic genera (BPP = 1). Additionally, one polytypic and six monotypic branches were also identified, all with 0.95 or greater BPP. Traditionally some of these clades have been recognized by a combination of meristic and morphological attributes, although without a phylogenetic framework (Allen and Robertson, 1994; Courtenay, 1961; Lindeman and Toxey, 2002; Mago, 1961; McKay, 2001).

Some of our findings are not novel, as previous phylogenetic analyses (Sanciangco et al., 2011; Tavera et al., 2012, 2011) have already revealed to some extent the failure of the former taxonomy to reflect phylogenetic relationships, therefore we emphasize novel results. Fig. 2 summarizes our generic phylogenetic classification including major modifications to previous non-phylogenetic taxonomies.

Our analysis resolves *Pomadasys* into five different lineages spread throughout Haemulinae, in contrast to previous studies (Sanciangco et al., 2011; Tavera et al., 2012) that have found *Pomadasys* in three branches. In all cases there is consensus for a convincing non-monophyly of this genus. The number and possible classification of the clades in which *Pomadasys* species (*sensu lato*) are to be allocated cannot be anticipated until a more inclusive sampling of all putative species of this paraphyletic assemblage are analyzed. We therefore do not propose taxonomic amendments on all of these branches, to avoid further taxonomic instability given the number of unrepresented taxa in our analyses (18 out of 35). Nevertheless, some progress can be made:

At the base of Haemulinae two well supported, sequentially nested

clades of *Pomadasys* (*sensu lato*) can be found; the first includes five “*Pomadasys*” like subclades (*P. perotai* + (*P. olivaceus* + *P. incisus*)) as the sister lineage of all other haemulines, followed by a larger clade of seven species, including the type species *P. argenteus*. In order to keep monophyletic groups concordant with taxonomic rules, the genus name must be determined by reference to the type species; in this case all nominal taxa included in the same clade as *P. argenteus* (Forsskål 1775) should be the only ones to be considered under the generic epithet of *Pomadasys* (*sensu stricto*).

Additionally, two strongly supported clades of two and three species, of exclusively New World putative *Pomadasys* (*sensu lato*), were recovered: *P. panamensis* + *P. macracanthus* and *P. branickii* + (*P. crocro* + *P. bayanus*) (Fig. 1). The former was resolved as the sister lineage to the remaining New World species, and the latter was found in a highly supported (BPP = 1) clade, sister to the branch containing ((*Haemulopsis* + *Conodon*) + *Xenichthys*).

Jordan and Evermann (1896a: 387), by original designation, selected *Pristipoma panamense* Steindachner, 1875: 36, (i.e. *Pomadasys panamensis*) as the type species of the genus *Rhencus* (Kottelat, 2013). We propose to restore this generic name to include both *P. panamensis* and *P. macracanthus*. Details for why *Pristipoma* is not eligible are found in the literature (Kottelat, 2013; Tavera et al., 2012).

Here we recapitulate taxonomic suggestions of Tavera et al. (2012) who proposed to resurrect *Rhenciscus* Jordan & Evermann, 1896, to include *P. branickii* and *P. crocro*. Our phylogenetic analyses not only corroborate the monophyly of this clade but also allow us to include the species *P. bayanus*.

The Galapagos endemic, *Orthopristis lethopristsis* was found nested between the monotypic *Isacia conceptionis* and *Microlepidotus* hence rendering *Orthopristis*, under its current definition, polyphyletic. Morphological attributes mainly related to the unique scaling pattern shared among the scalyfin grunt (i.e. *O. lethopristsis*) and *Microlepidotus* (Grove and Lavenberg, 1997; Jordan and Fesler, 1889) appear to be consistent with this finding.

The brownstriped grunt *Anisotremus moricandi* is considered a *bona fide* member of the genus *Anisotremus*; however, the generic status of this taxon rests on morphological similarities. *Anisotremus*, excluding *A. moricandi*, was recovered monophyletic (BPP = 1). Our data fails to consistently recover *A. moricandi* within this clade. Low support on this section of the tree (Figs. 1 and 2) prevents us from confidently identifying it as sister to *Anisotremus* (*sensu stricto*) so we exclude it and place it in its own genus, *Paranisotremus* new genus.

Previous studies found *Xenistius californiensis* related to *Haemulon chrysargyreum* and together they form the sister lineage of all remaining *Haemulon* (Sanciangco et al., 2011; Tavera et al., 2012). Sanciangco et al. (2011) concluded that *X. californiensis* should be treated as *Haemulon californiensis*, as they share the same diagnostic characters according to Jordan and Gilbert (1882) and Courtenay (1961). We differ from this decision adding that these morphological diagnoses did not attempt to assess monophyly of the mentioned taxa. There are different ways

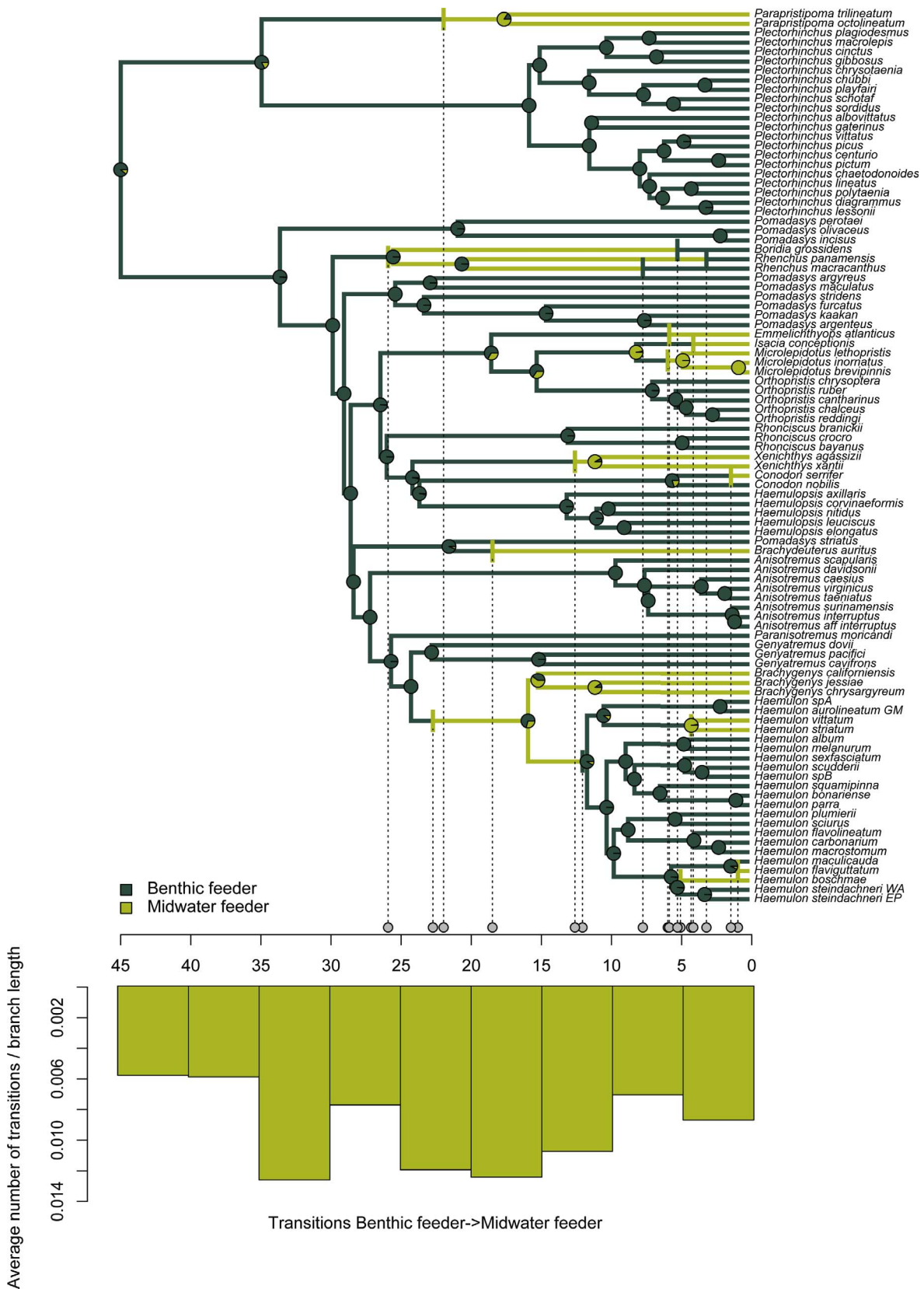
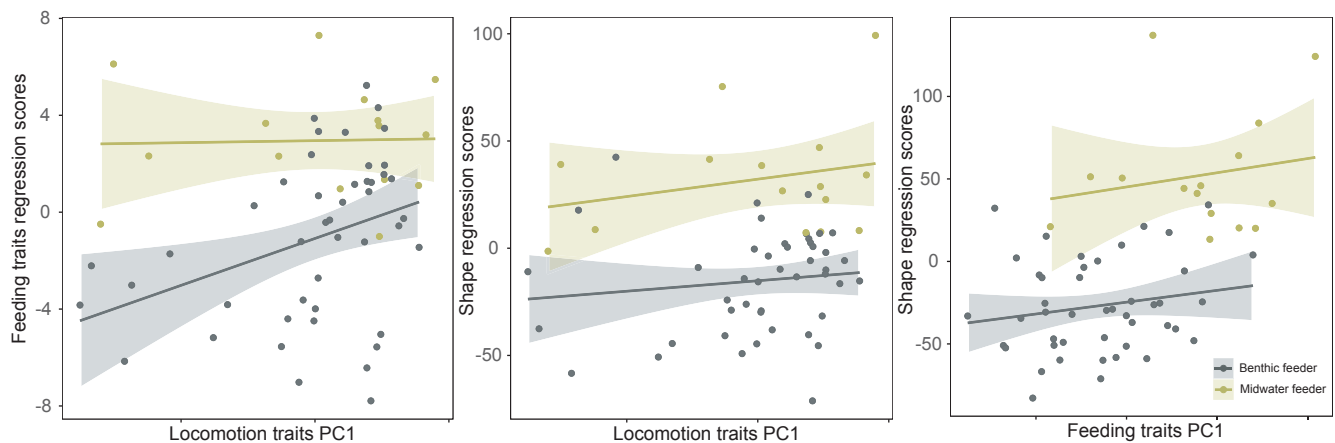


Fig. 4. Phylogenetic generalized least squares regression plots for different axes of functional and morphological diversity. The three panels represent all possible combinations among the components of the different data sets (i.e. feeding, locomotor, and shape) with 95% confidence intervals as shaded areas. The dashed line represent a non-significant correlation.

groups could be delimited taxonomically based on the phylogeny; our phylogenetic analyses resolve a strongly supported clade (*Xenistius californiensis* + (*Xenocys jessiae* + *Haemulon chrysargyreum*)) deeply

separated, yet, sister to all remaining species of *Haemulon* (Figs. 1 and 2). While our phylogenies could be consistent with the clade-naming presented in Sanciagco et al. (2011), we believe their scenario fails to





**Fig. 5.** (A) Ancestral-state-reconstruction analysis for the feeding mode evolution for the family Haemulidae. The colors correspond to their feeding type where dark gray = benthic feeder, light gray = pelagic feeder. Pie charts on nodes indicate the posterior probability support for each feeding type reconstruction. Vertical gray bars indicate the timing of transition events. (B) Bar graph indicating timing and amount of transitions summarized from 10,000 SIMMAP simulations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

recognize striking anatomical and ecological differences (Chirichigno and Cornejo, 2001; Courtenay, 1961; Grove and Lavenberg, 1997; Hobson and Chess, 1976; Jordan and Swain, 1884), and the deep split of these clades as resolved here (Figs. 1 and 2). Thus, we propose to classify each of the two lineages in their own taxa, *Haemulon* for the larger group and resurrect *Brachygenys* to include (*Xenistius californiensis* + (*Xenocys jessiae* + *Haemulon chrysargyreum*)).

As stated by the International Code of Zoological Nomenclature: “Priority of publication is a basic principle of zoological nomenclature”. Following this standard, the name *Brachygenys* (Poey (ex Scutter), 1868) Fem. *Haemulon taeniatum* Poey 1860. [synonym of *Haemulon chrysargyreum*, Günther, 1859] is available and older than *Xenistius* Jordan & Gilbert 1883; and *Xenocys* Jordan & Bollman 1890; therefore, we propose to resurrect it and use it for the three species included in this clade (i.e. (*Xenistius californiensis* + (*Xenocys jessiae* + *Haemulon chrysargyreum*))).

Fig. 1 represents the most current knowledge of the evolutionary relationships among grunt species. Fig. 2 condenses the new generic phylogenetic classification while Table 1 summarizes the proposed taxonomic changes.

#### 4.1. Revised generic classification

##### 4.1.1. Genus *Paranisotremus* n. gen. Tavera, Acero and Wainwright

*Type species.* *Haemulon moricandi* Ranzani 1842.

*Diagnosis.* This monotypic genus is diagnosed from other New World genera by the following combination of characters: Maximum body depth 37%–43% of standard length, frequently over 40%; six narrow white stripes over golden-brown background; a whitish J mark ventrally and posteriorly around the eye; a dark blotch on the posterior extreme of the opercle; one brown ocellus surrounded by whitish ring on the caudal peduncle; two brown spots dorsally on caudal peduncle; mouth red within, pharynx red; pelvic fins black; 7–8 rows of scales between lateral line and base of first dorsal spine; 16–17 pectoral rays; one of the smallest species of the family, reaching 18 cm total length.

*Etymology.* From the ancient Greek παρά (pará) meaning beside, next to, near, resembling. The name is in reference to the close appearance of the species to *Anisotremus*, which is the genus in which this species has been included for the last 35 years, since its redescription by Acero and Garzón (1982).

*Taxa and distribution.* The genus is monotypic, including only *P. moricandi* from Costa Rica to Brazil in the Western Atlantic (WA).

*Habitat.* Marine.

*Comments.* Although the placement of *Paranisotremus* within Haemulidae is not fully resolved, *Anisotremus sensu stricto* is strongly

supported as monophyletic when *P. moricandi* is excluded. If *P. moricandi* is sister to *Anisotremus* or to the clade composed by *Genyatremus* + *Haemulon* + *Brachygenys* still needs to be clarified.

##### 4.1.2. Genus *Brachygenys* Poey, (ex Scudder) 1868

*Type species.* *Haemulon taeniatum* Poey 1860.

Synonym of *Haemulon chrysargyreum* Günther 1859.

*Diagnosis.* This genus differs from its sister genus *Haemulon* by having a bigger ratio of eye diameter to snout length 1.7–2.7 versus 0.5–1.4. Generally, *Brachygenys* species have a smaller mouth (upper mandible 9–13% of SL), snout very short and obtuse (4–10% of SL), and a slender body (26–33% of SL). Chin with 2 pairs of pores, rear pores larger, and well separated, not in a hole, except for *B. chrysargyreum*. Spiny and soft dorsal fins completely separate or deeply notched. Adult silvery grey; head and body with 5–7 contrasting horizontal stripes along side; species reaching no more than 30 cm total length, usually 25 cm.

*Etymology.* From the Greek βραχυς (Brachy), short; γένος (genys), chin. The name makes reference to the small snout found in these species.

*Taxa and distribution.* The genus includes three species, one from southern Florida (USA) to Brazil including the Antilles in the Western Atlantic (WA) (*B. chrysargyreum*) and two in the Eastern Pacific (EP), *B. californiensis* (Steindachner, 1876) distributed in Central California (USA) to the Gulf of California (Mexico); and *B. jessiae* Jordan & Bollman 1890, endemic to Galapagos Islands (Ecuador).

*Habitat.* Marine.

*Comments.* Although *Xenocys jessiae* + *Haemulon chrysargyreum* + *Xenistius californiensis* could be included in *Haemulon*, as done by Sanciangco et al. (2011), we consider morphological and molecular evidence sufficient to place these species in their own genus.

##### 4.1.3. Genus *Rhencus* Jordan & Evermann 1896

*Type species.* *Pristipoma panamense* Steindachner 1876.

*Diagnosis.* This genus is diagnosed from formerly New World “*Pomadasys*” by the following combination of characters: Body oblong, depth 36%–43% of standard length; head 35–42% of standard length; snout 19–32% of head length; dorsal spines rather long, 17–22% of standard length; third dorsal spine much longer than the others; second dorsal spine short, less than half the length of the third (35–45%); pectoral fin very long, reaching anus and soft portion of dorsal fin. Dorsal fin with XI to XII spines, usually XII. Color silvery, a distinct dark blotch on opercle.

*Etymology.* ρογκός (snoring).

*Taxa and distribution.* This genus includes two species, both from the

Eastern Pacific (EP), from southern Baja California (Mexico), including the Gulf of California, to Tumbes (Peru).

*Habitat.* Marine, entering brackish estuaries.

#### 4.1.4. Genus *Rhonciscus* Jordan & Evermann 1896

*Type species.* *Pristipoma crocro* Cuvier 1830.

*Diagnosis.* This genus is diagnosed from formerly New World “*Pomadasy*” by the following combination of characters: Rather elongated body, depth 26–37% of standard length; head 30–38% of standard length; snout pointed, 24–42% of head length; dorsal spines low, 13–16% of standard length; fourth dorsal spine longer than the others; pectoral fin short, not reaching anus or soft portion of dorsal fin. Dorsal fin with XII to XIV spines, usually XIII.

*Etymology.* Diminutive of *ρογκος* (snoring).

*Taxa and distribution.* The genus includes three species, *R. crocro* from southern Florida (USA) to Brazil including the Gulf of Mexico and the Antilles in the Western Atlantic (WA) and two in the Eastern Pacific (EP): *R. branickii* (Steindachner, 1879) from southern Baja California (Mexico), including the middle and lower Gulf of California, to Paita (Peru); and *R. bayanus* Jordan & Evermann, 1898, with confirmed records from Mazatlan (Mexico) to Rio Tumbes, Peru.

*Habitat.* Marine, entering brackish estuaries, and also rivers and freshwater streams.

#### 4.2. Galapagos endemics

Five species of Haemulidae have been described as Galapagos endemics: *Orthopristis cantharinus*, *O. forbesi*, *O. lethopristis*, *Xenichthys agassizii*, and *Xenocys jessiae*. Two of these have their sister species in the Western Atlantic and not in the adjacent Eastern Pacific as might be expected (Figs. 1 and 3). *Orthopristis cantharinus* was found to be sister to *Orthopristis ruber*, a Southern Atlantic species and *Xenocys jessiae* is sister to *Haemulon chrysargyreum*, a widely distributed Western Atlantic species. This interesting pattern is also mirrored in sparids where *Archosargus pourtalesii*, a Galapagos endemic and the only member of this genus in the Eastern Pacific, appears to be closely related to *Archosargus rhomboidalis*, a Western Atlantic species. These phylogenetic patterns reveal interesting hidden biogeographic histories linking the Galapagos and Caribbean. Perhaps a common extinction event occurred in the Eastern Pacific eliminating species from several lineages, or a more ancestral relationship related to plate tectonics might be involved. This novel outcome creates a fertile ground for future studies.

The two species *Anisotremus interruptus* and *A. scapularis* have remote populations on the Galapagos archipelago, and both reveal substantial genetic isolation (Figs. 1 and 3). This finding also deserves further attention as taxonomic implications might be involved. If these two populations deserve a new taxonomic status it is unsettled and needs to be addressed using additional information.

#### 4.3. Divergence times

The divergence times estimated for grunts are comparable and consistent to those published in broader analyses (Betancur-R et al., 2013; Near et al., 2012), although this is expected as we drew our fossil calibrations from these previous works. Comparison of node ages among studies reveals only slight differences in the age estimates. The 95% HPD age estimates for the MRCA of all grunts ranged from approximately 54.7–42.3 Ma. These ages correspond to the Late Paleocene and Eocene, slightly after Paleocene/Eocene Thermal Maximum (PETM), 55 million years ago, a period of time characterized by a rapid rise of global temperatures, turnover in both marine and terrestrial biota, as well as significant changes in ocean chemistry and circulation (Kennett and Stott, 1991; Nunes and Norris, 2006). Crown ages for Haemulinae and Plectorhinchinae date to the mid Eocene extending into early and mid Oligocene, respectively. The Eocene–Oligocene transition was marked by noticeable trends of lineage extinction and

origination in both the terrestrial and the marine fossil record associated primarily with global climate change (Donovan et al., 2007; Ivany et al., 2000; Prothero, 1994).

Estimates of divergence times suggest that New World haemulids arose during the Eocene/Oligocene (95%HPD: 34.5–27 Ma). An initial and apparently rapid period of diversification, indicated by the short branches and the base of Haemulinae, occurred during the early and mid Oligocene followed by a period of slower diversification until the mid to late Miocene when another pulse can be identified (Fig. 1). Thus, it appears that the descendants of several modern lineages originated somewhat before or near the Eocene–Miocene transition approximately 23 Ma. Our age estimates suggest that the majority of reconstructed grunt speciation events date back to the Oligocene and Miocene, yet a few occurred during the Pliocene with some recent splits happening as recently as the last 2.5 my.

#### 4.4. Functional and morphological diversification

Morphological and functional diversity among grunt species appears to be linked to feeding ecology (Fig. 3). Benthic feeders tend to have wider mouths, higher mechanical advantage of lower jaw opening, greater jaw protrusion, shorter gill rakers, and a deep-bodied shape. Midwater feeders tend to be elongate and slender-bodied, with narrow mouths, shorter premaxilla ascending process, and long gill rakers.

Body shape differed sharply between species that feed in the two habitats, and it is significantly correlated with trophic and locomotion data sets, suggesting shape might be a good predictor of ecological functionality in haemulids. Feeding traits as a whole were significantly integrated with both locomotion traits and body shape (Fig. 4). Although correlated evolution among traits may constrain diversification to a limited range of combinations (Klingenberg, 2010), trait integration does not necessarily affect disparity of morphospace occupation (Goswami et al., 2014), though it may distribute variance along certain axes, typically those that offer least resistance to selection. This seems to apply to grunt morphospace occupation, where midwater feeders vary widely along PC2 of feeding and locomotion traits. Integration among traits also facilitates repeated evolution of morphologies (i.e. convergence) (Goswami et al., 2014; Klingenberg and Ekau, 1996), and we seem to see this in the repeated evolution of the elongate form in midwater lineages.

Benthic feeding by some species of grunts involves searching for prey that are buried in sand or mud, while in others species they feed on prey attached to the substrate. Among benthic-feeding species, a ventrally placed mouth and a deep body shape are common. The significant correlation between evolution of locomotion and feeding traits suggest a tighter constraint on the locomotion adaptations that are associated with the major axis of evolution in feeding. Among benthic feeders, the most active predatory species tend to have large mouths, high aspect ratio caudal fins and slender bodies, while sediment sifters are deep-bodied and have smaller mouths.

The benthic to pelagic axis has been a major axis of diversification in New World haemulids. The primary axes of overall body shape and feeding morphology each have a strong association with habitat (Fig. 3) and we estimated about 13 habitat transitions in the history of the group (Fig. 5). Feeding in the benthos is associated to a larger mouth and deeper body shape, while midwater fish are slender and have a smaller mouth with less protrusion. While each habitat harbors considerable diversity in morphology, it is clear that transitions between benthic and pelagic feeding modes have major consequences for haemulid morphological evolution.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jympev.2017.12.032>.

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