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SYMPOSIUM

The Evolutionary Continuum of Functional Homodonty to Heterodonty in the Dentition of *Halichoeers* Wrasses

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Synopsis Vertebrate dentitions are often collapsed into a few discrete categories, obscuring both potentially important functional differences between them and insight into their evolution. The terms homodonty and heterodonty typically conflate tooth morphology with tooth function, and require context-dependent subcategories to take on any specific meaning. Qualifiers like incipient, transient, or phylogenetic hornodon ty attempt to provide a more rigorous definition but instead highlight the difficulties in categoriz.ing dentitions. To address these issues, we recently proposed a method lor quantifying the function of dental batteries based on the estimated stress of each tooth (inferred using surface area) standardized lor jaw out -lever (inferred using tooth position). This method reveals a homodonty-heterodontyfunctional continuum where small and large teeth ...,rk together to transmit fon:es to a prey item. Morphological homodonty or heterodonty refers to morphology, whereas functional homodonty or heterodonty refers to transmission of stress. In this study, we use *Halichoeres* wrasses to explore how a functional continuum can be used in phylogenetic analyses by generating two continuous metrics from the functional homodonty- heterodonty continuum. Here "" show that functionally heterodont teeth have evolved at least 3 times in *Halichoeres* wrasses. There are more functionally heterodont teeth on upper jaws than on lower jaws, but functionally heterodont teeth on the lower jaws bear significantly more **stress. These nuance>s which have functional c.onseguence>s would be missed by binning entire dentitions into discrete** categories. This analysis points out areas worth taking a closer look at from a mechanical and developmental point of view with respect to the distribution and type of heterodonty seen in different jaws and different areas of jaws. These **dat>a on a small group of wrasses, suggest continuous dental variables can be a rich source of insight into the evolution** of fish feeding mechanisms across a wider variety of species.

Introduction

Vertebrates are spectacularly diverse in their ecology, behavior, and morphology, yet most vertebrates rely on the same structures to capture food: jaws and teeth (Estes and Williams 1984; Massare 1987; Davit-Beal et al. 2007; Jones 2009). The constraints and opportunities generated by, and from these structures, have been generated with both physical and mathematical modeling (Lucas and Luke 1984; Evans and Sanson 1998; Shergold and Fleck 2005; Anderson and LaBarbera 2008; Un r 2014). Predictions based on tooth shape alone produce incomplete anecdotes of functional diversity in the same dentition. The dentition of ambush predators such as *Ophiodon elongatr,s* are a great example; these fishes rely on a large tooth surrounded by many smaller teeth to maximize the damage delivered to a prey item (Gallowayet al. 2016; Mihalitsis and Bellwood 2019). The conical shape of their teeth does not matter as much for function as their

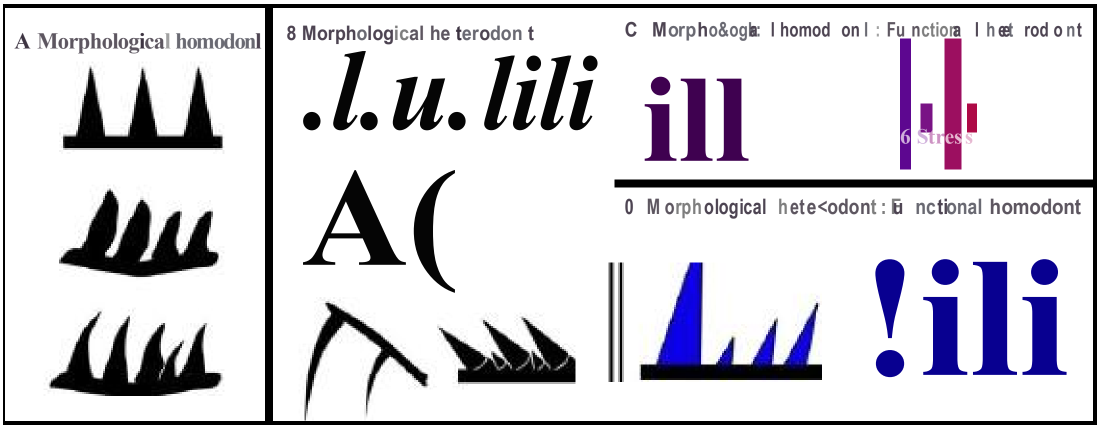

Fig. 1 Morphological versus functional hornodo . (A) Morphologic:aUy hornodo dentitiona ll teeth are siril r in shape or size compared to (B) morphologically heterodont dentition ha.ve some sort of regionalization il shape or size. A morphological cut off is hard to come byas slgfi!ficant changes il tooth shape are biased by ou r ni terpretation of de itions. Functio m l homodont¥ and heterodonty (C and D) uses changes in so-ess to draw an unambiguous line between tooth shape and tooth Lnction.

position. Generating a biomechanical framework for how particular tooth shapes and dentitions function is essential lo understanding how they evolve (Evans and Sanson 1998; Lucas 2004; Evans and Sanson 2005; Anderson and Labarbera 2008).

Teeth represent an information-rich opportunity to explore tendencies in developmental transitions, functional divergence, and even sexual selection For example, the unilateral tooth replacement in pacus and piranhas is a synapomorphy for the clade and represents a constructional constraint in maintaining an interlocked dentition (Berkovitz 1975, 1980; Kolmann el al. 2019). The morphology of the dentine in fossils of shark teeth provides new synapomorphies across orders and even pushes us to reconsider the origin of particular groups (Jambura el al 2020). Characterizing the entire dental battery as either homodonl or heterodonl has been used as a tool lo understand dental evolution for nearly a century (Cope 1888; Simpson 1936 ; Keene 1991; Schwartz 2013; Bertrand 2014; Conway el al. 2015; D'Amore 2015; Cullen and Marshall 2019). Most bony fishes are considered morphologically homodont and have a battery of similarly shaped and sized teeth (i.e., Fig. IA; Kenne 1991; Ungar 2014; Berkovitz and Shellis 2016). Morphological heterodonty is reserved for dentitions that have noticeable differences in shape or size (i.e., Fig. IB; Kenne 1991). For example, pacu, the herbivorous relatives of piranhas, have both incisiform and molariform teeth that are used lo distinguish genera (Berkovitz 1980; Kolmann el al 2019). The evolution of morphological heterodonty is consistently used in systematics often lo infer differences in prey processing (Kenne 1991; Becerra el al 2018). We explicitly do not assume that size and shape are the same as function-instead, we pose the question: do teeth that look alike actually function in the same way (Mihalitsis and Bellwood 2019; Cohen el al. 2020; Hulsey el al 2020)1

A lack of size or shape morphological diversity in a dental battery does not necessarily indicate a lack of functional diversity (Gregory 1933; Evans and Sanson 1998; Whitenack and Gottfried 2010; Anderson and Rayfeild 2012; Schwaru 2013; Mihalitsis and Bellwood 2019; Cohen el al. 2020). The morphologically homodonl dentition of piscivorous coral-reef fishes does not appear functionally diverse, but there is room for important functional decoupling in the jaws (Mihalitsis and Bellwood 2019). A fang al the front of the jaw moves al high velocity and ensures prey capture, and the large forces al the posterior fangs do the most damage (Mihalitsis and Bellwood 2019). Here, two similarly shaped teeth are functionally very different, owing to their position along the jaw. Morphological homodonty conceals phenotypic variation by only considering the dental battery in terms of shape and size. But if you care about dental function then stress is the important parameter, because stress predicts how much damage a tooth can do lo a prey item (Fraz.zetla 1988; Freeman and Weins 1997; Shimizu el al. 2005; Dean el al 2008; Clark and Summers 2012; Smits and Evans 2012; Schofield el al. 2016; Bergman el al. 2017; Marcus el al. 2017; Mihalitsis and Bellwood 2019; Cohen el al 2020). If stress is critical for understanding dental function, then il should also be critical for understanding the evolution of dental batteries. To address this problem, we need lo understand that broad dental characterization misses critical information in evolutionary comparisons, and we need a tooth by tooth metric that

Table 1 Specimm table: tist of species represe ed il ttiis study

Species	Museum	Cat. number	M orp hos ou rce DOI	Sea.no ire faci lity
Hokhoeres orgus	FMN H	FMNH 124452	da : 10.17602/M2/M57770	Kare4 F. Liem Bioimaging center
Hokhoeres binotopsis	FMN H	FMNH 75982	da : 10.17602M2M8 820	Kare4 F. Liem Bioimaging center
Hokhoeres &sp;/us	FMN H	FMN H n 29	da : 1 0. 1 7 602/M2/M56335	Kare4 F. Liem Bioimaging center
Ho&ichoeres hortzfek!ii	FMN H	FMN H 11 070 1	da : 10.1 7 602M2M5728	Kare4 F. Liem Bioimaging center
Hokhoeres hortulonus	FMN H	FMNH 12686	da : 1 0. 1 7 602/M2/M58197	Kare4 F. Liem Bioimaging center
Hokhoeres Jeucurus	FMN H	FMNH 126976	da : 10.1 7602/M2/M58195	Kare4 F. Liem Bioimaging center
Ho&ichoeres mo aw/)inno	FMN H	FMNH 65217	da : 10.17602/M2/M56339	Kare4 F. Liem Bioimaging center
Hokhoeres mefonochir	FMN H	FMNH 126991	da : 10.17602/M2/M58200	Kare4 F. Liem Bioimaging center
Hokhoeres po&s,;gmo	FMN H	FMNH 110 709	**da** : 10.17602/M2/M57006	Kare4 F. Liem Bioimaging center
Ho&ichoeres prosepeon	FMN H	FMN H 1 20 1 60	**da** : 1 0.1 7 602/M2/M57775	Kare4 F. Liem Bioimaging center
Hokhoeres rdvn M&	FMN H	FMN H 121 20	da : 1 0. 1 7 602/M2/M57772	Kare4 F. Li = Bic,;,:naq;,q c...te,

All CT scans are free to download from morphosotrce.org and represented here by DOI. FMN H (fi eCd Museum of Natural Histo.-y, ChicagQ IL. USA).

incorporates stress into our quantification of dentitions.

Qualitative categori2ations of dental characters, such as morphological homodont, macrodont, or edentulate, do not capture functional variation in dentitions (Ruber et al. 1999; Shimada 2002; Sansom 2016). Discrete categori2ations summarize and discard information in an effort to simplify den- titions for comparative analysis. Continuous charac- ters allow a finer scale comparison among continuous environmen tal, ecological, and gene ex- pression data than can be achieved with categorical functional characters (Garamszegi 2014; Adams and Collyer 2018). The concept of functional homodonty can transform anatomical measures of individual teeth into a quantitative metric of dental battery function. A morphological homodont has teeth of "similar" shape and size, but functionally homodont teeth exert similar stresses regardless of shape or size. Where morphological heterodonty captures shape re- gionalitation across individual teeth, functional het- erodonty highlights teeth with stresses that exceed a threshold across a dentition (Cohen et al. 2020).

Functional hornodonty is a biomechanical descrip- tion of the dentition that has the potential to be combined with phylogenetic information to reveal evolution of specific dentitions or feeding strategies. To demonstrate that functional homodonty-h eter- odonty continuum provides meaningful insight into the evolution of dentitions, we applied the method to 11 of the ~80 species of *Halichoeres* wrasses(fam- ily I.abridae). In this study, we use three metrics to summarize the functional homodonty method We calculate (I) the proportion of functionally homo- dont to functionally heterodont teeth to identify individuals with the most potential for function diversity across their dental battery, (2) the average squared residual of functional homodonty as a mea- sure of functional diversity in the dental battery, and (3) we compare the average squared residual off unc- tioml homodonty to the proportion of functionally heterodont teeth to highlight different types of het- erodonty. Our goal is to lay the groundwork for the further exploration of a biomechanical metric that can be extended to other taxa and detect functional diversity that is otherwise lost in discrete categori2a- tions of dentitions.

Methods

Study species

The genus *Halichoeres* is common on rocky or soft reefs in the Indian, Atlantic, and Pacific oceans where they feed primarily on small benthic inverte- brates (Randall 1967; Clifton and Motta 1998). They have a full dentition on both upper and lower jaws ranging from 10 to IS teeth, including upper and lower anteriorly pointing fangs, and a pair on the posterior process of the maxilla. The modest size of the group, a well resolved phylogeny,similar hab- itat, and purported generalist diet make *Halichoeres* a useful group to explore the functional homodonty metric in an evolutionary context

Measurements and scans

All CT *scans* were downloaded from the Scan All Fishes project on Morphosource.org (Table I) these *scans* were origimDy presented in Evans et al. (2019). Each specimen was scanned at Friday Harbor la boratories' Karel F. Uem Memorial Bio-Imaging Facility using a Bruker 1173 SkyScan (Micro Photonics Inc., Allentow n, PA, USA). AD specimens

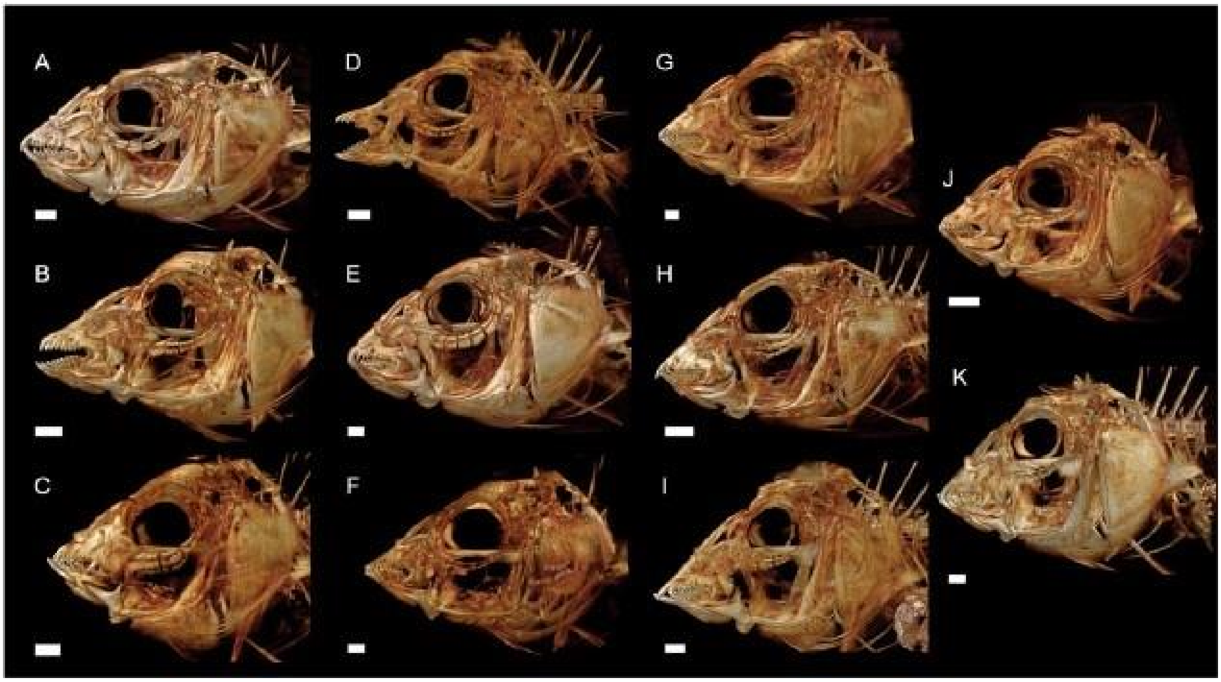

Fig. l CT scan re nder-i s of 11 species of *Holichoeres* wrasses represm ti different tooth morphologies. (AJ *H. hortzfeldl* (BJ *H. rlchmond(* (CJ *H.* poci,stlgmo, (DJ *H. melonochlr,* (E) *H. dlspilus.* (F) *H. orgus.* (GJ *H. proso loo.* (HJ *H. mo c u lp/Mo,* (IJ *H. hortllllonus.* OJ H.Jeucurus. and (KJ *H.* llrotopsis. Scale bar is set to 1000µm.

were scanned between 34 and 35.5*µm* voxel size at 65 kV and 123 uA. A total of II *Halichoeres* wrasse species were chosen for this study representing individuals with varying tooth morphologies across the three *Halichoeres* radiations (Fig. 2). Digital surface models of the jaws and teeth were created in Amira version 5.2.2 (Visage Imaging. Inc., Richmond, VIC, Australia). Surfaces were then exported to Meshlab (Visual Computing la b, ISTI-CNR, Pisa, Italy) where jaw length, tooth height, radius, and tooth positions were measured.

The stress of each tooth was calculated following the principles of simple lever mechanics. Using the surface area of a cone we approximate the surface area of each tooth by measuring tooth height-defined by the total length from tooth tip until the tooth meets the jawbone-and tooth radius (Fig. 3):

$$\text{Surface area} = n r (r + (\underline{Jh'} + r')) \qquad \text{(I)}$$

To establish a basic relationship between surface area and tooth stress we use the entire height of the tooth. Following the guide of puncturing mechanics, stresses should be concentrated at the tip of the tooth; however, our metric is not meant to establish where an individual tooth bears the greatest stress but instead to identify patterns in stress across teeth in the same dentition Therefore, we ignore expected changes in stress from the tip to the base of each tooth in order to establish a relationship between the variation of tooth morphologies in a dental battery and *stresses* along the jaw. The standardization of tooth morphology allowed us to ignore curvature and damage yielding an idealized tooth surface area, which we used to calculate *stress* under different conditions (Crofts and Summers 2014).

Considering that teeth are on a lever, we had to first establish the amount of force a tooth is predicted to exert based on its position.

$$F_{.,,,} = F_{;.} * sjn(a) * (\frac{folever)}{\underline{0'1t4}\ \underline{lever}} \qquad (2)$$

Our model assumes that the mechanical advantage, and force at the input lever is the same across jaws and that the input muscle force and input lever arm are the same for all teeth on the jaw. We modeled the upper jaw (premaxilla) with a static bite point assuming that it was in the most retracted position of its sliding position in the anterior jaws linkage (Westneat 2004). The model also assumes a single angle of muscle input force, with jaws in closed position, and no changes in gape were modeled. We simplified our system by assuming that Ftn

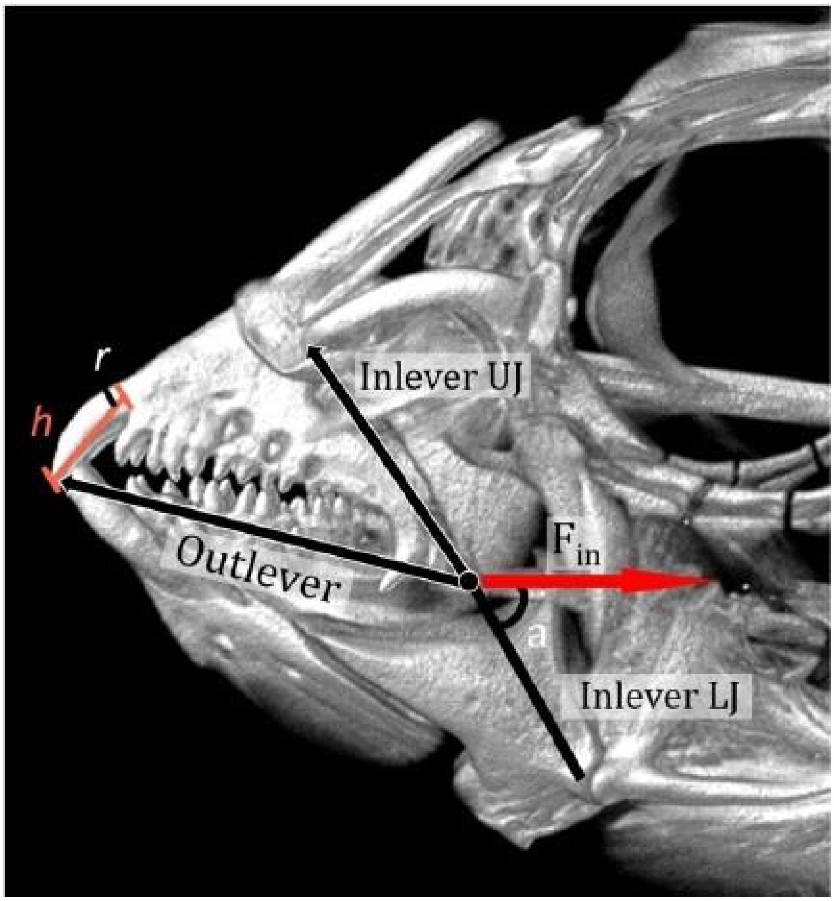

Fig. 3 Measuring stress: Skull of *H. hortzfeldU*, showing tooth morphology and FH calculation protocol. Using tooth surface area derived from linear measurements measured from CT scans in Meshlab we calculate the stress of each tooth in the dental battery considering the force and jaw position. The force equations are derived from lever mechanics.

and F_{in} ratios were constant in all calculations, generating F_{tooth} equation where F_{tooth} is equivalent to F_{in} (Equation 3).

$$F_{tooth} = \frac{F_{in} * P_{tooth}}{L_{jaw}} \qquad (3)$$

where F_{tooth} is the force at a particular tooth, F_{in} is the input force (set to 1N in our model), P_{tooth} is the position of the tooth in question, and L_{jaw} is the length of the jaw. We calculated the stress at the surface of each tooth by dividing the calculated force on a tooth (F_{tooth}) by the surface area (Equation 4).

$$\sigma = \frac{F_{tooth}}{SA_{tooth}} \qquad (4)$$

where σ is stress and SA_{tooth} is the tooth surface area.

We expressed the position of each tooth and the height of each tooth as a percentage of jaw length. We compared the stress at each tooth across jaws, individuals, and species and compared the stress residuals across teeth. Normalized stresses were inputs for a bootstrap analysis for determining a functional homodonty threshold.

Generating a functional homodonty threshold

In an ideal functional homodont, all teeth experience the exact same stress, regardless of size or position (Cohen et al. 2020; Table 2). This is an unrealistic expectation for real specimens: we are unlikely to calculate identical stress values for each tooth even in a functional homodont, given biological and technical variance. Instead, for functionally homodont dentitions, we expect stress values along the jaw to not differ significantly. Our challenge with testing functional homodonty in real organisms, therefore, is defining reasonable tolerance limits for significant variations in stress.

To do this, we calculated stress residuals for each dentition by subtracting the median stress for a

Table 1 **Important definitions for the functional homodonty method**

Term	Definition
Functional homodonty method	Method detailed in Cohen et al. (2020) for (1) using tooth surface area and position to calculate tooth stresses through the transmission of force and (2) estimating a threshold for functionally heterodont teeth by bootstrapping stress values from multiple dentitions.
Functionally homodont teeth	All of the teeth in a dentition have statistically similar stresses that do not exceed a set threshold of stress
Functionally heterodont teeth	One or more of the teeth in a dentition has statistically different stresses that exceed a set threshold of stress from the majority of the dentition
Idealized functional homodont	All of the teeth in a dentition bear the exact same median stress
Idealized functional heterodont	All of the teeth in a dentition bear stresses that exceed the functional heterodonty threshold
Functional homodonty-heterodonty continuum	A continuum, ranging from the idealized functional homodont to the idealized functional heterodont onto which all dentitions can be mapped using the functional homodonty method

dentition from each stress value and dividing by median stress (i.e., centering and scaling to median stress), allowing for comparison across dentitions. An idealized functional homodont would experience the same stress on each tooth regardless of size or position, resulting in residuals of 0 for each tooth in that dentition. To determine a threshold for functional homodonty, we bootstrapped a residual stress distribution per Cohen et al. (2020). Half of the teeth were randomly subsampled without replacement from a dentition and normalized residuals calculated; this procedure was repeated 10,000 times for each dentition. The resulting distribution of residuals was centered around 0, with small clusters of extreme values representing teeth that experienced ∼1.8 times or more stress than the median for a given dentition (Fig. 4). The multimodal structure of bootstrapped residuals pointed us to clustering techniques to determine threshold values for functionally homodont/heterodont teeth. Our first implementation of this method (Cohen et al. 2020), used *k-means* to distinguished between high and low residual peaks (Maechler et al. 2019). In *Halichoeres* the wider range of bootstrapped residuals with extreme values resulted in poor fits using k-means. Instead, we used the more robust k-medoids clustering algorithm which uses data points as cluster centers (Maechler et al. 2019). Because k-medoids is considerably slower than k-means and could not be run on our entire sample of bootstrapped residuals at once, we performed the k-medoids clustering (with $n = 2$ clusters) on a random subsample of 5000 residuals 100 times, defining the threshold as the mean of the two resulting cluster centers. The resulting threshold ranged from 1.64 to 1.88 times median stress, with an average of 1.8 times median stress (Fig. 4, inset).

Summary statistics and phylogeny comparison

We generated two metrics from the normalized stress calculations, each designed to emphasize a specific aspect of the dentition: the average squared residual and proportion of functional heterodont teeth. To measure the degree of functional difference among teeth from the same battery, we calculated the average squared residual (where residuals = stress - median stress) for stress across a jaw. We also calculated the proportion of individual teeth in each battery that differed in function from the majority; unlike the variation in stress, this metric ignores the fold-difference of stress but emphasizes regionalization. We visualized these continuous traits on a time-calibrated phylogeny (Aiello et al. 2017; Supplementary Fig. S1) using the contMap function from the phytools R package contMap (Revell 2012). The phylogeny of 340 labrid species was time-calibrated using fossil data (Aiello et al. 2017), pruned down to the local clade containing the set of taxa studied here (Supplementary Fig. S1) and then pruned to the set of species studied here for comparative analysis using the R package ape (Paradis et al. 2004).

Results

Functional homodonty method

In 11 species and more than 440 teeth, 17 teeth bear stresses that exceed the homodonty threshold (Fig. 4, dashed line). While all of the 11 species of *Halichoeres* represented in this dataset have at least one tooth that exceeds the functional homodonty threshold, three species had especially high values for at least one of the metrics we calculated: *Halichoeres dispilus*, *Halichoeres melanochir*, and *Halichoeres maculipinna* (Fig. 6). Each have a single

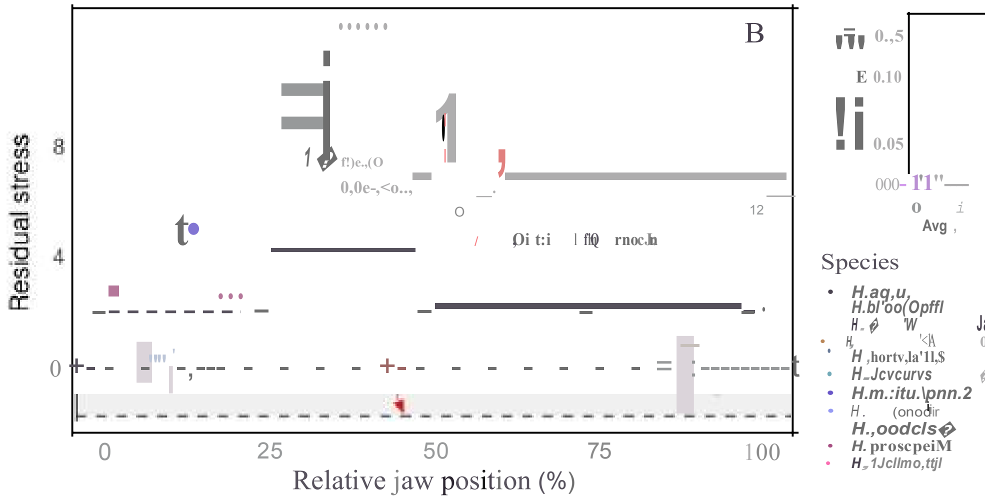

Fig. 4 Functional homodalty metric. (A) teeth frcm the jaws of 11 Holld>oeres. Teeth above the da<hed lile <!)(ceed the funct kmal homodalty thre<hold (BJ de fned by the bootstrappilg of reskluals. We then use k-mediods to ga,erate a biologically relevant **threshold (red dashed lite). (C) Co rison of the propo rtion of functionally heterodont teeth to the average squared residual il four species of *Holichoeres* wrasse to highlight the tendencies emerging from this riso n. (1) High propo rtion hnc tionaUy heterodont** teeth: low resi dual. (2) Low propo n!oo of heterodalt teeth high residual. and (3) High proportloo of IJnctlonally heterodoot teeth: high residual

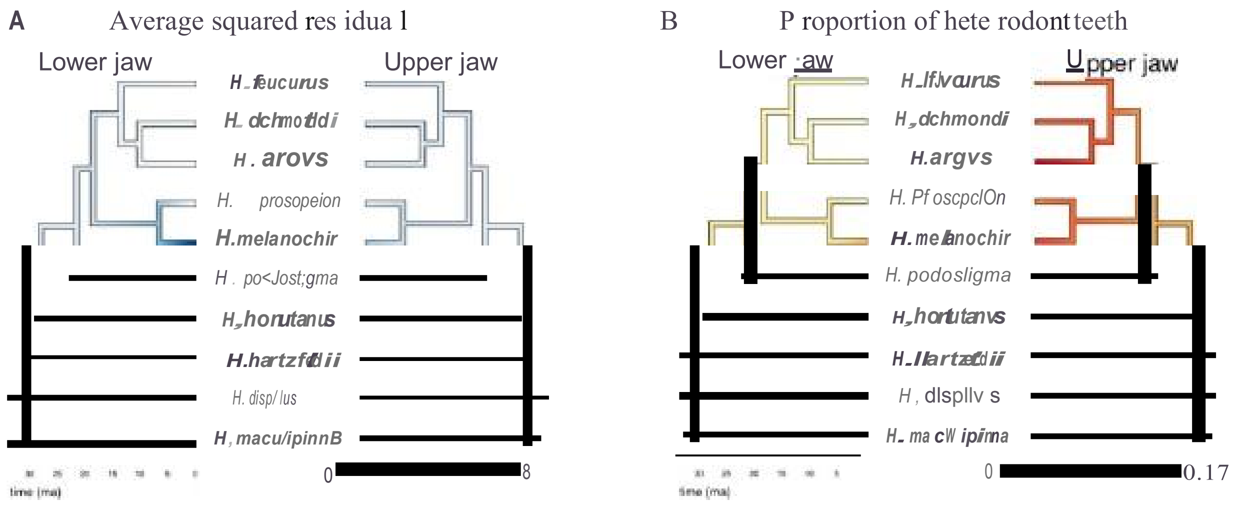

Fig. 5 Phylogeny co ri'lg the upper and lower jctNs in 11 species of *Hc1ktloeres.* Thereare more function.aUy heterodont teeth in the i.pper jaws than the lower jaws, represented by a greater number of heterodo teeth (A). But LnctionaUy heterodont teeth in the lower jaws have a bigger ct and are represented by a larger residua.I (8). No te, *H.bJropt.J1* is removed from the logate tic c risons as stresses were only calcUated il the lower jaw.

tooth on the lower jaw that bears 12 times the median stress of that dentition, far exceeding the functional homodonty threshold of 1.8 times median stress. While *H. mactl1ipinna* had no teeth bearing stresses that high, the specimen we analyzed had 2 of 12 teeth on the upper jaw exceed the functional homodonty threshold, the highest proportion of any of the dentitions we measured (Fig. 4A). The upper and lower jaw fangs of *H. macc111ipinna* occlude far beyond the anterior end of the jaws with hardly any curvature. The species *H. melanochir* most closely resembles a morphological homodont and *H. dispil11s* has two sets of large canines that extend far beyond the end of the premaxilla or dentary while the rest of their teeth are similar in size (Fig. 2C-E).

Across all 11 species, functionally heterodont teeth were more frequent on the upper jaws. While fewer teeth on the lower jaws exceeded our functional heterodonty threshold, those that did typically had much higher residuals, in some cases bearing up to

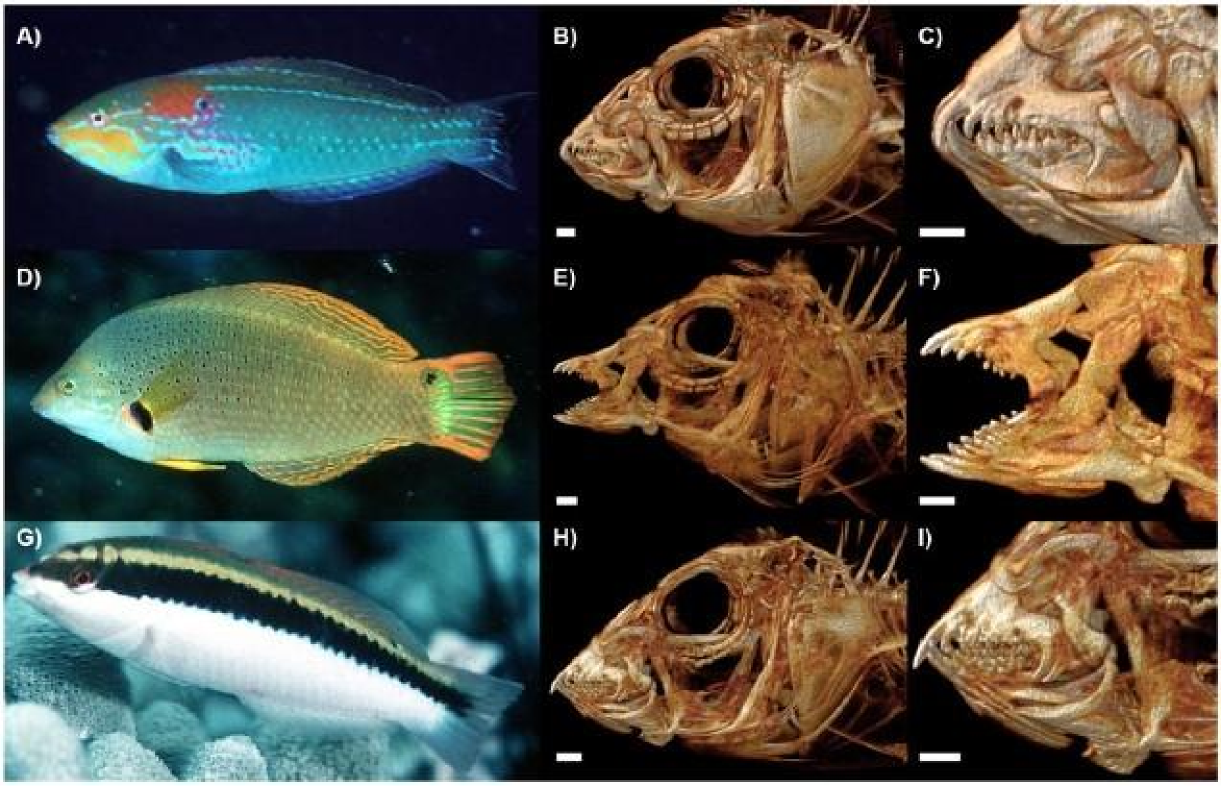

Fig. 6 f u>ctlooally heterodalt species of ***Hollcho<ro�*** (A-<:) *H. dlspilus.* (D-F) *H. molenochlr,* (G- *H.* poci,S!Jgmo. Live photos for all three species downloaded from AshBa.se.org and provided by J.E. Randall Sca le bar is set to 1000 µm.

twice the stress of the teeth on the upper jaw of the same fish (Figs. 4C and 5, especially *H. dispi111s* and *H. melanochir).*

There are differences in the magnitude of functionally heterodont teeth across all 11 species. For instance, *H. podostigma* has a singular functionally heterodont tooth on its lower jaw that barely exceeds the heterodonty threshold. This tooth bears 2.4 times the median *stress* of the rest of the dentition. By comparison, *H. melanochir* has several teeth that bear between 4 and 12 times the stress of functionally homodont teeth in the same dentition.

Proportion versus average squared residual of **functionally heterodontteeth**

Ancestral state reconstruction suggests the ancestral *Halichoeres* had a small number of functiomily heterodont teeth, and these were more likely on the upper jaw than the lower. The three species with high numbers of heterodont teeth or high average squared residuals were in two of the three *Halichoeres* clades. Along the continuum of functional homodonty to heterodonty, we find three tendencies (Fig. 5). First, some taxa departed from functional homodonty because of one or two exceptional teeth in a battery of otherwise functionally homodont teeth. This is represented by large residuals and a small proportion of functionally heterodont teeth (H. *dispil11s).* Next, are fishes with regionali2.1tion of function, these have small residuals but a high proportion of functionally heterodont teeth (*H. maculippina).* Finally, a dental battery could have large and small teeth interspersed evenly across the jaws as in *H. melanochir* (Fi g. 4Aand C) which leads to a high proportion of functionally heterodont teeth combined with high residuals.

Discussion

The biomechanical function of teeth is largely dependent on tooth morphology, orientation, position along the jaw lever from front to back, and the dynamic forces of the jaw muscles driving them into a prey item (Bare! 1982; Westneat 2003; Anderson et al 2016). Here we present a way to calculate the biomechanical function of teeth in jaws of labrid fishes from the perspective of their geometry and the relative bite stresses they exert Our central conclusion is that *Halichoeres* wrasses have a wide diversity of tooth arrangements that lend to functional homodonty. However, some species have strikingly functionally heterodont teeth-either a few teeth or regions of teeth with disparate function. There will always be some level of heterodonty at the tips of the teeth across any dentition, but our metric draws a clear line between functional homodonty and functional heterodonty.

There are dentitions that have distinct regionalization, where many teeth are quite similar to one another, but patches are performing very different tasks (Cohen et al 2020; Mihalitsis and Bellwood 2019). In contrast, there are dentitions where one or a few teeth are radically different from the rest of the dental battery. In the first case, there will be a large number of functionally heterodont teeth, but a low average squared residual, and in the second case there will be a few functionally heterodont teeth, but they will have a very high squared residual. In *Halichoeres* wrasses two species have extremely functionally heterodont teeth, and they arrive at heterodonty by different means. In *H. melanochir,* the teeth are strongly regionalized with a high proportion of functionally heterodont teeth, whereas in *H. dispilus* just two large canines in the upper jaw dictate functional heterodonty leading to high residuals (Figs. 4A and 5).

Our method converts a categorical trait, morphological homodonty, into a continuous one, functional homodonty, creating opportunities for more nuanced analyses and directing phylogenetic and biomechanical hypotheses in new directions (Shimada 2002; Westneat and Alfaro 2005; Kolmann et al. 2019; Hulsey et al. 2020). Adding the perspective of phylogeny bears two different fruits. First, we can identify three apparently independent evolutions of functional heterodonty: *H. dispilus, H. melanochir,* and *H. maculipinna* (Fig. 6). Second, our ancestral state reconstruction implies an ancestral *Halichoeres* wrasse had a small number of functionally heterodont teeth, and the proportion of functionally heterodont teeth is variable over evolutionary time. A metric for functional heterodonty also allows us to generate computed derivatives that reveal trends and potentially important information about selective pressures (Linde et al. 2004; Kolmann et al. 2019). The higher proportion of functionally heterodont teeth on upper jaws than lower jaws may be due to the upper jaw being supported by the cranium, while the lower jaw is a cantilever beam (Powlik 1995; Linde et al. 2004; Westneat 2004; Westneat and Alfaro 2005; Grubich et al. 2008; Smits and Evans 2012; Olsen and Westneat 2016). Also, the magnitude of functionally heterodont teeth is larger in the lower jaw than upper, perhaps because of mobility in the lower jaw relative to the entire body of the fish (Figs. 4 and 5). How a species arrives at functional heterodonty should point biomechanists in very different directions when asking about the functional consequences of teeth.

We were excited to find such disparate dentitions, and three independent derivations of heterodonty, in just 11 species of a genus of wrasse that all occupy similar nearshore, shallow water, coral reef habitats, and have all been assigned the same broad dietary niche (Randall and B(lhlke 1965; Clifton and Motta 1998; Fulton and Bellwood 2002; Jones 2007). Implementing this analysis across a broader phylogenetic and ecological range of wrasses will lead to discovery of further, heretofore cryptic variation in dental function that we expect will inform natural history and diet studies. The *Halichoeres* radiation may be an intriguing area of the labrid phylogeny to explore in more detail, as the genus is not monophyletic, with 80 species spread across three clades, with other genera such as *Macropharyngodon, Thalassoma,* and *Goris* interspersed among them (Westneat and Alfaro 2005). The hogfishes and tuskfishes (*Bodianus, Choerodon,* and relatives) often have extraordinarily large, recurved canines and regionally specialized teeth, yet their close relatives such as *Pse,idodax* and *Q epric,,s* possess jaws specialized for browsing or planktivory, suggesting an interesting trajectory of tooth evolution. The cheiline wrasses are also diverse in tooth morphology, jaw mechanics and dietary preferences (Westneat 1995) and are the sister-clade to the parrotfishes, offering another area in which to explore the evolution along the functional homdonty-heterodonty continuum.

Even in this small, and not particularly diverse clade of wrasses, there are some examples of dentitions that warrant further examinations. *Halichoeres le1u:1m1s* is morphologically homodont, but the teeth in the upper and lower jaw occlude with a degree of precision that is not common in fishes (Kolmann et al. 2019). Physical models of teeth, made from high-resolution CT scans of actual dentitions, could highlight advantages of this unusual tooth arrangement (Evans and Sanson 2003; Qian et al 2013; Crofts and Summers 2014). There are visually arresting fanged dentitions, such as *H. horwlanus,* which do not cross the threshold for functional heterodonty, but nevertheless have teeth that suggest some differences in function (Fig. 2A). Careful natural history observations of differences in behavior of species with prominent fangs may reveal how and when these fangs are deployed. Other biomechanical models, such as Mandiblever, take into account tooth angle and its interaction with gape angle across a realistic bite (Westneat 2003). Teeth are, in some sense, an endpoint in a series of modules which determine function (Evans and Sanson 2003; Lucas 2004; Anderson and Rayfeild 2012; Kolmann et al 2019}- the powerful, subdivided adductor musculature, through tendons and ligaments connecting jaw elements, to the levers and linkages of the jaws, and even the seemingly insignificant dental ligaments securing tooth to jaw combine to ensure that the tip of the tooth transmits sufficient stress to penetrate prey.

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Data availability statement

All CT data used in this study are publicly available and free to download from morphosource.org in the Scan All Fishes project.

Supplementary data

Supplementary data available at *ICB* online.

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