Syst. Biol. 71(1):1–12, 2022

DOI:10.1093/sysbio/syab012
Advance Access publication February 23, 2021

Phylogenomic Analysis of Concatenated Ultraconserved Elements Reveals the Recent Evolutionary Radiation of the Fairy Wrasses (Teleostei: Labridae: *Cirrhilabrus*)

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Received 29 May 2020; reviews returned 11 February 2021; accepted 17 February 2021
Associate Editor: Bryan Carstens

Abstract.—The fairy wrasses (genus *Cirrhilabrus*) are among the most successful of the extant wrasse lineages (Teleostei: Labridae), with their 61 species accounting for nearly 10% of the family. Although species complexes within the genus have been diagnosed on the basis of coloration patterns and synapomorphies, attempts to resolve evolutionary relationships among these groups using molecular and morphological data have largely been unsuccessful. Here, we use a phylogenomic approach with a data set comprising 991 ultraconserved elements (UCEs) and mitochondrial *COI* to uncover the evolutionary history and patterns of temporal and spatial diversification of the fairy wrasses. Our analyses of phylogenetic signal suggest that most gene-tree incongruence is caused by estimation error, leading to poor resolution in a summary-coalescent analysis of the data. In contrast, analyses of concatenated sequences are able to resolve the major relationships of *Cirrhilabrus*. We determine the placements of species that were previously regarded as *incertae sedis* and find evidence for the nesting of *Conniella*, an unusual, monotypic genus, within *Cirrhilabrus*. Our relaxed-clock dating analysis indicates that the major divergences within the genus occurred around the Miocene–Pliocene boundary, followed by extensive cladogenesis of species complexes in the Pliocene–Pleistocene. Biogeographic reconstruction suggests that the fairy wrasses emerged within the Coral Triangle, with episodic fluctuations of sea levels during glacial cycles coinciding with shallow divergence events but providing few opportunities for more widespread dispersal. Our study demonstrates both the resolving power and limitations of UCEs across shallow timescales where there is substantial estimation error in individual gene trees.[Biogeography; concatenation; gene genealogy interrogation; gene trees; molecular dating; summary coalescent; UCEs.]

The wrasses (family Labridae) are among the largest and most successful of the marine teleostean radiations. With over 600 valid species (Parenti and Randall 2000; Fricke et al. 2020), the family is second only to the gobies (family Gobiidae) in marine species richness (Randall et al. 1990; Fricke et al. 2020). Despite their cosmopolitan distribution, it is within coral reefs that the wrasses attain maximum diversity. Here, they are known not only for their impressive diversity in coloration and form but also in functional specialization and ability to exploit novel trophic guilds (Cowman et al. 2009; Evans et al. 2019; Huertas and Bellwood 2020).

While there have been several efforts to resolve the evolutionary relationships among the wrasses (Westneat and Alfaro 2005; Cowman et al. 2009; Cowman and Bellwood 2011), contention persists at almost all levels of the labrid phylogeny, ranging from contested monophyly (Kaufman and Liem 1982; Schultz 1978; Bellwood 1994; Parenti and Randall 2000) to widespread systematic disarray at the intrafamilial level (Westneat and Alfaro 2005). One group in critical need of systematic revaluation is the pseudocheilines, an informal group of wrasses comprising around 100 species from six genera: *Cirrhilabrus*, *Conniella*, *Paracheilinus*, *Pseudocheilinus*, *Pseudocheilinops*, and *Pteragogus*.

Among the pseudocheilines, the fairy wrasses (*Cirrhilabrus*) are of particular systematic interest. With 61 species, they account for nearly 10% of all extant labrids (second only to the polyphyletic *Halichoeres*; see Barber and Bellwood 2005). The genus consists of small, brightly colored fishes found mostly on low-complexity rubble slopes adjacent to coral reefs, at depths of 10–250 m. Although sequential hermaphroditism and sexual dimorphism are common among labrids (Warner 1984; Kuiter 2010), it is in the fairy wrasses that these traits are most conspicuous. In contrast to the females, males are very colorful and are known for their exuberant nuptial displays. Their iridescent brilliance and underwater courtship performances have attracted considerable interest not only among labrid systematists but also among underwater photographers and aquarium fish collectors (Kuiter 2010; Tea et al. 2016).

The evolutionary relationships of the fairy wrasses have been difficult to resolve, leaving open questions concerning their diversification and evolutionary success. Previous phylogenetic studies have relied on nucleotide sequences of the mitochondrial *COI* gene (Tea et al. 2016, 2018b, 2020; Victor 2016). However, these have been met with limited success, in part due to the extensive sharing of *COI* haplotypes

among the fairy wrasses, even between species that are morphologically or geographically separated. Furthermore, morphological characters diagnosing species are often phylogenetically uninformative, with several of these characters being autapomorphic or homoplasious, or showing substantial intraspecific variation (Tea et al. 2016, 2020). These factors have made *Cirrhilabrus* one of the more phylogenetically recalcitrant groups of labrids, with scrutiny of color patterns or diagnoses based on a combination of characters being the only way to separate certain members of the genus.

The genus attains a large but asymmetric geographic distribution spanning the Indo-Pacific, with over half of the known species restricted to the Coral Triangle. For many species of *Cirrhilabrus*, analyses of mitochondrial DNA have inferred relationships that are incongruent with patterns of biogeographic distribution, species-level coloration, and morphological characteristics (Victor and Randall 2014; Allen et al. 2015; Tea et al. 2016). This situation, where high levels of species diversity are not reflected in mitochondrial DNA, is typical of taxa that have either evolved rapidly or are undergoing large-scale introgression (Harris et al. 2018; Hench et al. 2019). However, neither of these hypotheses has been thoroughly investigated, and little is known regarding the spatio-temporal evolution of the fairy wrasses.

The challenges in reconstructing the evolutionary history of the fairy wrasses can potentially be overcome by using a phylogenomic approach (Zhang et al. 2019; Cowman et al. 2020), such as the targeted capture of ultraconserved elements (UCEs) (Faircloth et al. 2012). Analyses of UCE data have shown great promise in resolving evolutionary relationships across vertebrates, including fishes at both shallow (DiBattista et al. 2018; Ludt et al. 2019) and deep evolutionary scales (Faircloth et al. 2013; Smith et al. 2015; Alfaro et al. 2018; Faircloth et al. 2020). However, the low information content of individual UCEs and incongruence between the UCE gene trees can pose problems for phylogenomic analyses (Gatesy and Springer 2014; Xi et al. 2015; Meiklejohn et al. 2016) and other downstream analyses that utilize the resulting trees such as estimation of divergence times using molecular dating.

Using an integrative phylogenomic approach that combines UCEs and mitochondrial *COI*, we explore the efficacy of UCEs in resolving the evolutionary history of the fairy wrasses. Our data set includes all pseudocheiline genera, including the monotypic *Pseudocheilinops* and *Conniella*, the latter a rare and enigmatic taxon investigated here in a phylogenetic context for the first time. We compare methods of phylogenomic inference based on the summary coalescent versus concatenation and investigate gene-tree estimation error caused by low phylogenetic information content. Our study provides new insights into the drivers of species diversity in a challenging taxonomic group, demonstrating both the resolving power and limitations of UCEs and their ability to capture the details of recent evolutionary history.

Materials and Methods

Taxon Sampling and DNA Sequencing

We sampled 39 of the 61 valid species of *Cirrhilabrus* (64% taxon coverage) for the target capture of UCEs. For 28 of these species, along with 10 additional species not included in our UCE sampling, we obtained publicly available sequences of mitochondrial *COI*. In combination, the UCE and mitochondrial data provided 80% taxon coverage across the genus *Cirrhilabrus*. We included the following pseudocheiline genera as outgroup taxa, following the relationships proposed by Westneat (1993): *Paracheilinus, Pseudocheilinus, Pseudocheilinops*, and *Pteragogus*. We also include the monotypic *Conniella* for a complete representation of the pseudocheilines.

Tissue samples were preserved in 80–100% ethanol and stored at −20°C prior to extraction using a DNeasy Blood and Tissue kit (Qiagen, Hildren, Germany). Library preparation, enrichment, and sequencing were performed by Arbor Biosciences (Ann Arbor, MI, USA) following methods described by Quattrini et al. (2018). Following target-capture enrichment, target-enriched libraries were sequenced on one lane of Illumina HiSeq 2500 (100 bp PE reads). A detailed description of taxon sampling and library preparation, as well as a complete list of tissues, sampling locations, and museum voucher information, is presented in the Supplementary Material available on Dryad at https://doi.org/10.5061/dryad.4tmpg4f6q.

Demultiplexed Illumina reads were processed using PHYLUCE (Faircloth 2016). To investigate the potential impacts of missing data, we assembled two UCE supermatrices based on loci that were represented in at least 75% of all sampled taxa, as well as a more conservative threshold of 95%. The 75% occupancy matrix consists of 991 UCE loci (330,550 bp) and the 95% occupancy matrix consists of 47 UCE loci (14,920 bp) from 38 ingroup taxa and 11 outgroup taxa. To test for model violations, which can cause systematic errors in gene-tree inference, we tested for compositional heterogeneity and substitution saturation using PhyloMAd (Duchêne et al. 2018). Further details of filtering, trimming, UCE assembly statistics, and model testing are in the Supplementary Material available on Dryad.

Phylogenomic Analyses

In order to improve taxon coverage, we assembled data sets based on concatenated sequences of the 75% occupancy UCE matrix and mitochondrial *COI* (Supplementary Tables S2–S5 available on Dryad). In total, the concatenated sequence alignment had a length of 331,202 bp. To evaluate the effects of missing data, we analyzed four concatenated data sets: 75% occupancy UCE + *COI* matrix; 75% occupancy UCE matrix; 95% occupancy UCE matrix; and the most variable 20% of the UCE loci (variable-loci UCE matrix; see expanded

methods in the Supplementary Material available on Dryad). We analyzed all data sets using maximum likelihood in IQ-TREE v1.6.12 (Nguyen et al. 2015) and Bayesian inference in ExaBayes (Aberer et al. 2014) (details provided in the Supplementary Material available on Dryad).

To account for gene-tree incongruence among loci, we analyzed the UCE data set using the summary-coalescent method in ASTRAL-III (Zhang et al. 2018). We inferred the species tree under a range of conditions (see Supplementary Material available on Dryad), including ASTRAL analyses of all 991 UCE gene trees inferred from the 75% occupancy matrix. We then analyzed the data after contracting branches in gene trees with less than 10%, 20%, and 30% bootstrap support. We performed ASTRAL analyses of a combined data set that comprised gene trees for all 991 UCEs + mitochondrial *COI*, and of the variable-loci UCE matrix. Topological distances between the various trees inferred using summary-coalescent and concatenation approaches were calculated using the normalized Robinson–Foulds metric using the R package phangorn (Schliep 2011). We also examined concordance between the gene trees and the concatenation-based species tree using PhyParts (Smith et al. 2015).

We conducted a gene genealogy interrogation (GGI; Arcila et al. 2017), to test topological hypotheses for five species complexes in *Cirrhilabrus* whose relationships were consistently poorly resolved in all summary-coalescent analyses: the *rubriventralis*, *filamentosus*, *cyanopleura*, *punctatus*, and *temminckii* complexes. In this analysis, we examined all 15 possible unrooted topologies for these five groups, using constrained maximum-likelihood searches for each of the 915 UCE loci (76 UCE loci were excluded from this analysis because of missing data). Site likelihood scores for all of the trees were compared using the approximately unbiased test (Shimodaira 2002). A full description of the gene genealogy interrogation is given in the Supplementary Material available on Dryad.

Phylogenomic Dating and Biogeographic Analyses

We used MCMCTree in the PAML package (Yang 2007) to perform a Bayesian dating analysis of the concatenated 75% occupancy UCE + *COI* matrix. Because our aim was to infer divergence times for closely related species, we chose not to employ deep fossil-based calibrations that would require the inclusion of distantly related taxa. Available labrid fossils for calibration include species from several distantly related lineages (summarized by Cowman and Bellwood 2011; Bellwood et al. 2019), for which no UCE data are available. Instead, we employed secondary calibrations from a well resolved, time-calibrated labrid phylogeny (Cowman et al. 2009). This involved two node calibrations: crown age of the pseudocheilines (*Pteragogus* vs. all other taxa, 25.7–49.8 Ma); and the divergence between *Pseudocheilinus* and *Paracheilinus* + *Cirrhilabrus* (10–34 Ma). These were implemented as uniform priors with soft bounds (Yang and Rannala 2006).

Ancestral biogeographic ranges were estimated for the time-calibrated phylogeny using the R package BioGeoBEARS (Matzke 2013). Biogeographic provinces were delineated following those described by Kulbicki et al. (2013), with modifications based on the contemporary distributions of *Cirrhilabrus*. We used the corrected Akaike information criterion to compare three biogeographic models: dispersal, extinction, and cladogenesis model (DEC; Ree and Smith 2008); dispersal-vicariance model (DIVA-like; Ronquist 1997); and BayArea-like model (Landis et al. 2013). Details of the phylogenomic dating and biogeographic analyses are given in the Supplementary Material available on Dryad.

Results

Phylogenomic Analyses: Concatenation vs Coalescence

Maximum-likelihood analysis of the concatenated 75% occupancy UCE + *COI* matrix yielded trees with well-supported nodes along the backbone of *Cirrhilabrus*, with monophyly of all species complexes (Fig. 1a). Except for taxa *incertae sedis*, the inferred relationships at deeper nodes were consistent with those previously inferred on the basis of mitochondrial DNA (Fig. 1b; Tea et al. 2020). This tree topology was congruent to the maximum-likelihood and Bayesian trees inferred from the 75% occupancy UCE matrix (Supplementary Fig. S1a,d available on Dryad), but with the additional *Cirrhilabrus condei* complex placed as the sister lineage to the *Cirrhilabrus filamentosus* complex. Maximum-likelihood and Bayesian trees inferred using the 95% occupancy UCE matrix and the variable-loci UCE matrix were less well resolved, with the *C. filamentosus, Cirrhilabrus rubriventralis, Cirrhilabrus cyanopleura*, and *Cirrhilabrus temminckii* complexes not recovered as monophyletic (Supplementary Fig. S1b,c,e,f available on Dryad). Analyses of concatenated UCE loci were able to resolve the relationships among species within all respective complexes, an outcome that was not achievable using *COI* sequences alone (Fig. 1c).

In contrast with the results of our analyses of concatenated UCE loci, phylogenomic analyses using the summary-coalescent approach in ASTRAL yielded poorly resolved trees. Across these analyses, monophyly was only supported for the *Cirrhilabrus exquisitus, Cirrhilabrus scottorum, Cirrhilabrus lunatus, Cirrhilabrus bathyphilus*, and *Cirrhilabrus lubbocki* complexes (Supplementary Fig. S2a–f available on Dryad). The relationships among polyphyletic complexes were not improved with contraction of branches with low bootstrap support in the gene trees (Supplementary Fig. S2b–d available on Dryad) when only a subset of most variable loci was used (Supplementary Fig. S2e available on Dryad), or with the inclusion of the *COI* gene tree (Supplementary Fig. S2f available on Dryad).

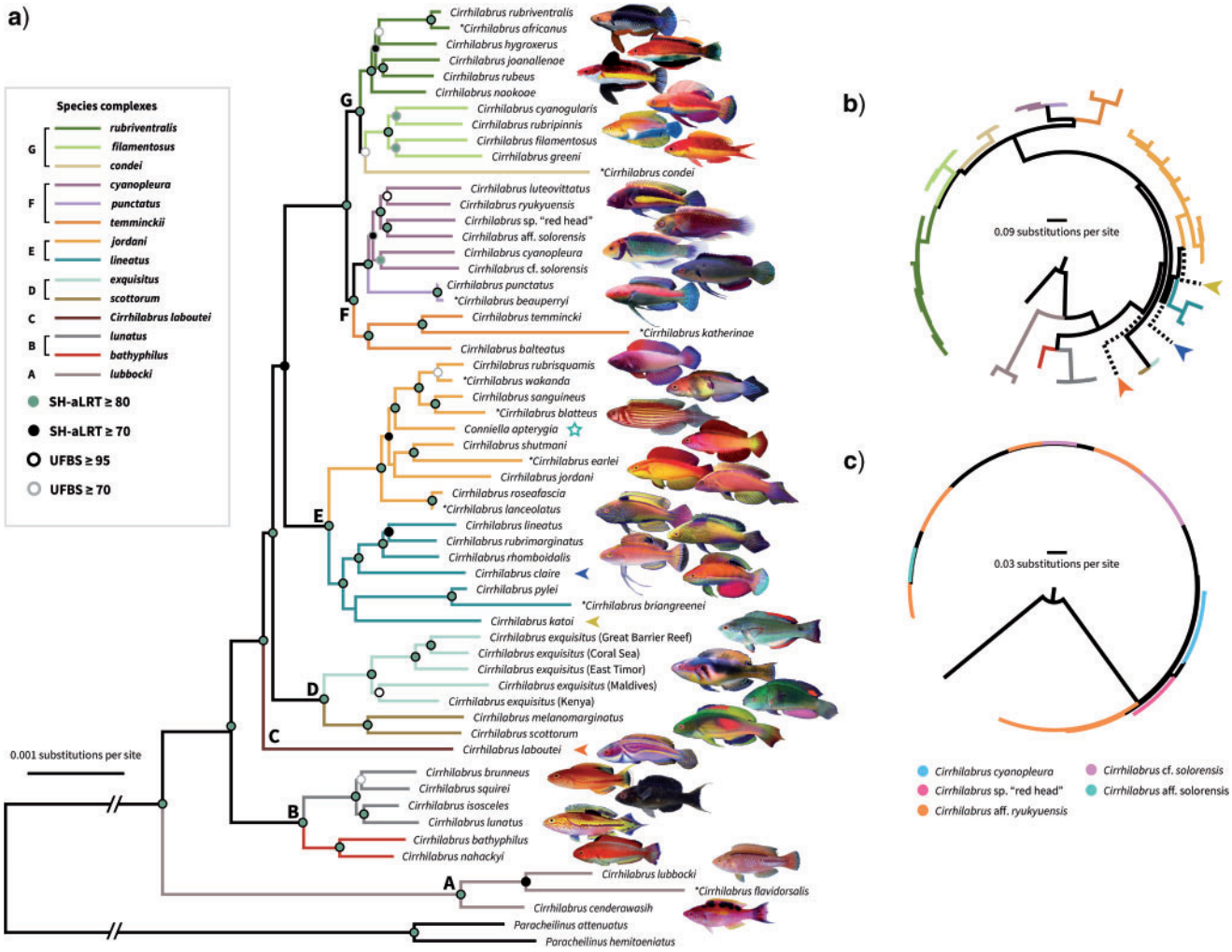

FIGURE 1. a) Maximum-likelihood phylogenetic tree of *Cirrhilabrus*, inferred using the 75% occupancy UCE + mitochondrial *COI* matrix. Asterisks indicate species that are represented by only *COI*. Open star indicates nesting of the monotypic *Conniella*. The outgroup genera *Pseudocheilinus*, *Pseudocheilinops*, and *Pteragogus* have been pruned from the tree. Circles at nodes indicate levels of SH-aLRT and UFBS support. SH-aLRT = Shimodaira-Hasegawa-like approximate likelihood ratio test.; UFBS = ultrafast bootstrapping. This phylogenomic approach has resolved previously intractable relationships among several species and the placements of those that were uncertain in analyses of mitochondrial *COI*. [b) Tree of *Cirrhilabrus* relationships, inferred from mitochondrial *COI*, adapted from Tea et al. 2018b, 2020]. Arrows indicate placement of taxa *incertae sedis* in both trees. c) Mitochondrial *COI* gene tree demonstrating sharing of haplotypes for several members of the *Cirrhilabrus cyanopleura* complex. Photographs by G. R. Allen, E. Fleishauer, M. P. Hammer, R. H. Kuiter, J. E. Randall, Y. K. Tea, and B. C. Victor.

While the number of parsimony-informative sites for each UCE locus ranged from 0 to 54, most loci contained 20 or fewer informative sites (Fig. 2a). Only five UCE loci had more than 40 informative sites, and only four loci had the minimum number of informative sites needed to resolve relationships of the species tree given that the fully resolved tree has 43 internal branches. We found no evidence of model violations among the UCE loci. Trees inferred using the summary-coalescent approach had topologies that were generally dissimilar to each other and to the trees inferred from concatenated data (Fig. 2b). This is likely to be due to most UCE gene trees having low average bootstrap values (~45–55%; Fig. 2c), with no gene tree having an average bootstrap value exceeding 70%, and with nearly all having topologies discordant with the underlying species tree (Supplementary Fig. S3a available on Dryad). In contrast, the topologies of the trees inferred from concatenated data were more similar to each other, even between those inferred using maximum likelihood and Bayesian inference, and between trees from which we pruned species represented by only *COI* sequences.

Our GGI analysis of the five most problematic species complexes showed that topological hypothesis H_0 had the highest probability (185 tests in favor) and statistical support ($P < 0.05$). This result corroborates the relationships inferred using the concatenated UCE data set. All of the alternative hypotheses (H_1–H_{14}) received negligible support (Fig. 2d).

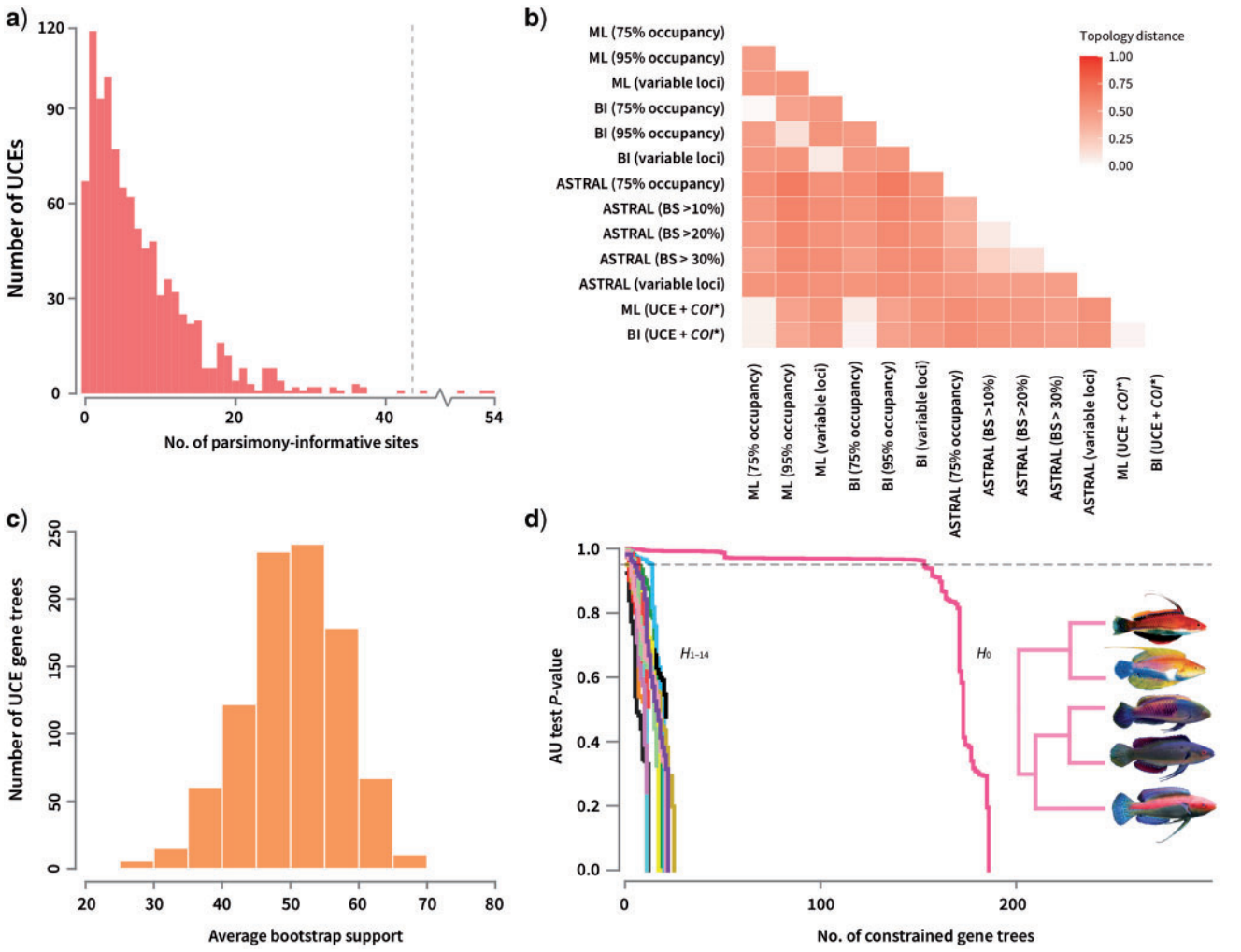

FIGURE 2. a) Plot of numbers of parsimony-informative sites for all UCE loci. The dashed line represents the minimum number of informative sites needed to resolve a species tree with 43 internal branches. b) Heat map of normalized Robinson–Foulds topological distances between trees inferred from different data sets and using different methods of analysis. Topological distances increase with color intensity. Asterisks indicate trees from which taxa represented only by *COI* sequences have been pruned. c) Plot of average bootstrap support across individual UCE gene trees. d) Gene genealogy interrogation applied to UCE loci. Colored lines represent each of the 15 possible unrooted topologies ($H_0 - H_{14}$) based on the five sampled species complexes (*rubriventralis, filamentosus, cyanopleura, punctatus*, and *temminckii* complexes). Values on x-axis represent cumulative number of UCE gene trees supporting each hypothesis with highest probability and their associated *P*-values (y-axis). Values above dashed line indicate hypotheses that are statistically significant ($P < 0.05$). H_0 indicates the highest-ranking hypotheses (represented by the inset tree topology).

Phylogenetic Relationships

Our maximum-likelihood and Bayesian analyses of the concatenated 75% occupancy UCE + *COI* matrix were able to resolve relationships among the fairy wrasses (Figs. 1a and 3a). All species complexes were recovered as monophyletic and formed seven major lineages, which we designate as Lineages A–G. In all analyses, *Conniella* was inferred to be deeply nested within *Cirrhilabrus*, in particular within the *Cirrhilabrus jordani* complex. The successive sister genera of *Cirrhilabrus* are *Paracheilinus, Pseudocheilinus*, and *Pseudocheilinops*. *Pteragogus* was found to be the sister lineage to all remaining pseudocheilines.

The maximum-likelihood and Bayesian trees were congruent across almost all nodes, except for relationships in Lineage G, where the placement of the *C. condei* complex was not resolved with confidence (Fig. 3b). Relationships of the previously *incertae sedis Cirrhilabrus claire, Cirrhilabrus katoi*, and *Cirrhilabrus laboutei* were resolved with high node support. Both *C. claire* and *C. katoi* were placed within the *Cirrhilabrus lineatus* complex, whereas *C. laboutei* was found to occupy a monospecific sister lineage to a group comprising Lineages D–G.

We resolved the phylogenetic relationships of several species for which mitochondrial DNA showed little to no variation (Fig. 1b), in particular those from the *C. rubriventralis, C. filamentosus, C. cyanopleura*, and *C. lunatus* complexes. However, not all nodes within these complexes were well supported, in

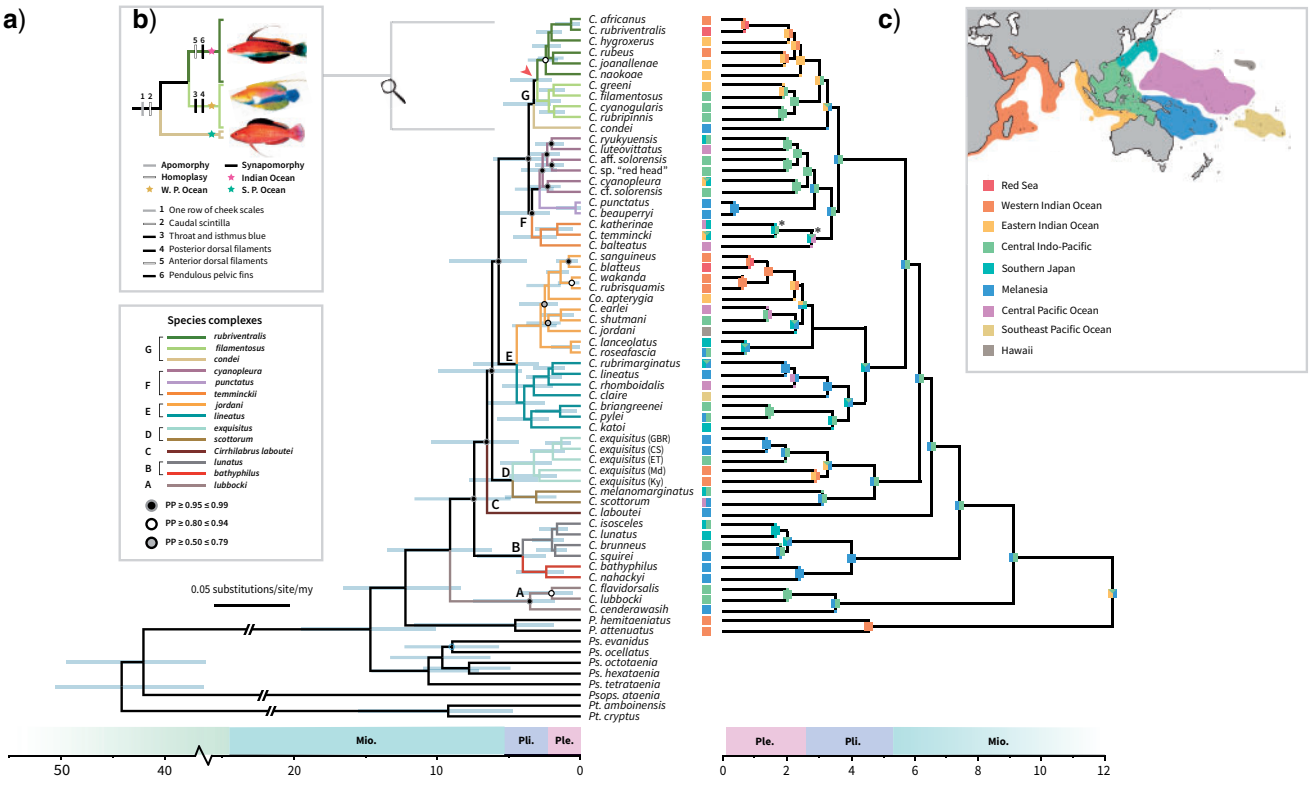

FIGURE 3. a) Time-calibrated phylogeny of *Cirrhilabrus*, inferred using a Bayesian relaxed-clock analysis of the 75%-occupancy UCE + mitochondrial *COI* matrix. All outgroup taxa are shown. Node bars represent 95% credibility intervals for node ages. Arrow indicates point of topological difference from the maximum-likelihood tree. GBR = Great Barrier Reef; CS = Coral Sea; ET = East Timor; Md = Maldives; Ky = Kenya. b) Cladogram for component species complexes of Lineage G, along with selected character states. c) Most probable ancestral ranges in the genus *Cirrhilabrus*, inferred using a BayArea-like model in BioGeoBEARS. Outgroup taxa have been pruned from the tree. Squares at nodes represent the most probable ancestral areas, or a combination of most probable areas. Unless specified (with an asterisk), the relative probability of areas or area combinations for all nodes were ≥35%. Squares at bases of terminal branches leading to tips represent most probable ancestral ranges immediately after a cladogenetic event. Squares at tips represent present-day distributions, with colors corresponding to biogeographic regions. Photographs by B. D. Greene, R. H. Kuiter, and B. C. Victor.

particular the positions of *Cirrhilabrus hygroxerus* in the *C. rubriventralis* complex, *Cirrhilabrus luteovittatus* + *Cirrhilabrus ryukyuensis* in the *C. cyanopleura* complex, and *Cirrhilabrus brunneus* + *Cirrhilabrus squirei* in the *C. lunatus* complex. All analyses found strong support for deep divergences between populations within the *C. exquisitus* complex, which are separated into the Indian Ocean and Pacific Ocean clades (Figs. 1a and 3a).

Timescale of Diversification and Historical Biogeography

Our Bayesian relaxed-clock analysis places the crown age of the pseudocheilines at 44.2 Ma (95% credibility interval [CI] 33.4–51.4 Ma). The split between *Paracheilinus* and *Cirrhilabrus* was estimated at 12.2 Ma (95% CI 8.2–16.3 Ma), in the mid to late Miocene (Supplementary Table S1 available on Dryad). The crown age of *Cirrhilabrus* was estimated at 9.1 Ma (95% CI 5.9–13 Ma), with several major divergences occurring between 5.7 and 7.4 Ma (Lineages B–E). Together, these lineages account for more than a third of all *Cirrhilabrus* species. Lineages F and G account for nearly all remaining species of *Cirrhilabrus*, diverging from each other approximately 3.6 Ma (2.1–5.6 Ma). These deeper divergences within *Cirrhilabrus* were succeeded by a set of cladogenetic events leading to several species complexes, occurring between 3.3 and 4.7 Ma around the Miocene–Pliocene boundary (Supplementary Table S1 available on Dryad). The topological differences in Lineage G between the Bayesian and maximum-likelihood trees had a small effect on most of the divergence-time estimates across the tree, including the crown age of the pseudocheilines (mean age of 44.2 vs. 43.8 Ma; Supplementary Fig. S3b,c available on Dryad).

In the BioGeoBEARS analysis, we found that the BayArea-like model had the highest support based on the corrected Akaike information criterion (BayArea-like: 370.7; DEC: 374.3; DIVA-like: 376.0). Under this model, the most recent common ancestor of *Cirrhilabrus* occurred in an area comprising the central Indo-Pacific and Melanesia (Fig. 3c). These areas were inferred for all nodes along the backbone of the tree, suggesting a common area of origin for many of the major lineages

of *Cirrhilabrus*. We resolve biogeographic histories for several taxa occurring in peripheral regions, including the western Indian Ocean, Hawaii, and the southeast Pacific Ocean. Our reconstruction of ancestral locations supports at least five independent invasions of the Indian Ocean by the *C. rubriventralis, C. filamentosus, C. cyanopleura, C. jordani*, and *C. exquisitus* complexes, via the boundaries of the central Indo-Pacific and Indian Ocean. In the *C. rubriventralis* complex, this occurred around 3 Ma (95% credibility interval 1.8–4.5 Ma) and was followed by expansion into the western Indian Ocean and dispersal into the Red Sea (*C. rubriventralis*).

The widespread *C. exquisitus* is also represented by populations occurring in the western Indian Ocean, but the ancestral area of origin for this complex remains unresolved due to a lack of representation from the eastern Indian Ocean. For the same reason, the biogeographic history of the *C. jordani* complex remains unresolved. The ancestral location for the Hawaiian endemic *C. jordani* occurred in an area comprising several regions of the western and southwestern Pacific Ocean. From these regions, southern Japan was inferred as the most likely ancestral area leading to cladogenesis and subsequent occupancy of Hawaii. The ancestor of the southeastern Pacific *C. claire* was placed in Melanesia.

Discussion

Phylogenomic Analyses

Our phylogenomic analyses of concatenated UCE loci have resolved major relationships among the fairy wrasses, revealing that the genus has an evolutionary history originating in the Pacific Ocean but involving multiple invasions of the Indian Ocean. In contrast, we found that summary-coalescent analyses of our data set yielded poor phylogenetic resolution, with several species complexes found to be nonmonophyletic. This result is consistent with those of several previous analyses of UCE data that have compared concatenation and summary-coalescent approaches, particularly in groups of organisms that underwent recent divergences (Meiklejohn et al. 2016; Longo et al. 2017; Ochoa et al. 2015).

In contrast with some previous findings (Longo et al. 2017), we found that contraction of poorly supported branches in the gene trees and targeted analyses focusing on informative loci did little to improve resolution in our species trees. This outcome is likely to be due to poor resolution in individual gene trees (Xi et al. 2015). Analysis of these data using a summary-coalescent approach led to trees that were topologically dissimilar to each other, even when gene trees with low information content were excluded. In contrast, trees inferred using a concatenation approach had relatively more consistent topologies, even between those obtained using reduced data sets and different methods of phylogenetic inference.

Coalescent theory predicts that lineages evolving under a combination of short internal branches and large effective population sizes have phylogenetic histories that are prone to incomplete lineage sorting (Degnan et al. 2009; Arcila et al. 2017). For taxa that diverged rapidly or recently, these conditions can lead to gene trees that are discordant with the underlying species tree. To investigate this possibility, we performed a GGI focusing on the relationships among five of the most poorly resolved species complexes in *Cirrhilabrus*, inferred on the basis of summary-coalescent approaches. The GGI results support the topology that is congruent with the relationships inferred using the concatenated UCE data set, as well as those of previous studies (Tea et al. 2018b).

On an individual level, the topologies of gene trees inferred from UCE data do not match that of the concatenated species tree, with nearly all of the relationships found to be incongruent. However, our tests of model adequacy did not detect any model violations, which can lead to errors in estimates of gene trees and species trees (Jeffroy et al. 2006; Whelan et al. 2015). Our results suggest that gene-tree incongruence is driven by a lack of phylogenetic information in individual UCE loci, supporting previous assertions that a concatenation approach is preferred over summary-coalescent approaches when estimation error is the dominant cause of gene-tree incongruence (Gatesy and Springer 2014; Bryant and Hahn 2020; but see Jiang et al. 2020). Nonetheless, we cannot exclude the possibility that our inference based on concatenated data has been misled by the effects of incomplete lineage sorting and interspecific gene flow. This should be looked for between closely related species within species complexes, given that the monophyly of most *Cirrhilabrus* complexes are well supported on the basis morphology and juvenile and terminal male coloration patterns (Kuiter 2010), and mitochondrial DNA. While incongruence between species trees and gene trees in rapidly diversifying taxa is not uncommon due to short internal branches, these same evolutionary histories can complicate the inference of gene trees by not allowing enough time for nucleotide substitutions on these branches. For this reason, we urge caution in interpreting whether coalescent or concatenation approaches might be more biased as a result of these factors.

Phylogenetic Relationships among the Fairy Wrasses

Our phylogenomic analyses of UCE loci have resolved some relationships that could not be determined on the basis of mitochondrial and/or morphological evidence. In particular, we find mutual monophyly of all species complexes and infer strongly supported relationships among species within the *C. rubriventralis, C. filamentosus, C. cyanopleura*, and *C. lunatus* complexes. We note, however, that taxonomic representation in these complexes was incomplete. For example, the putative sister species of *C. hygroxerus* from the *C. rubriventralis* complex, *Cirrhilabrus humanni* and

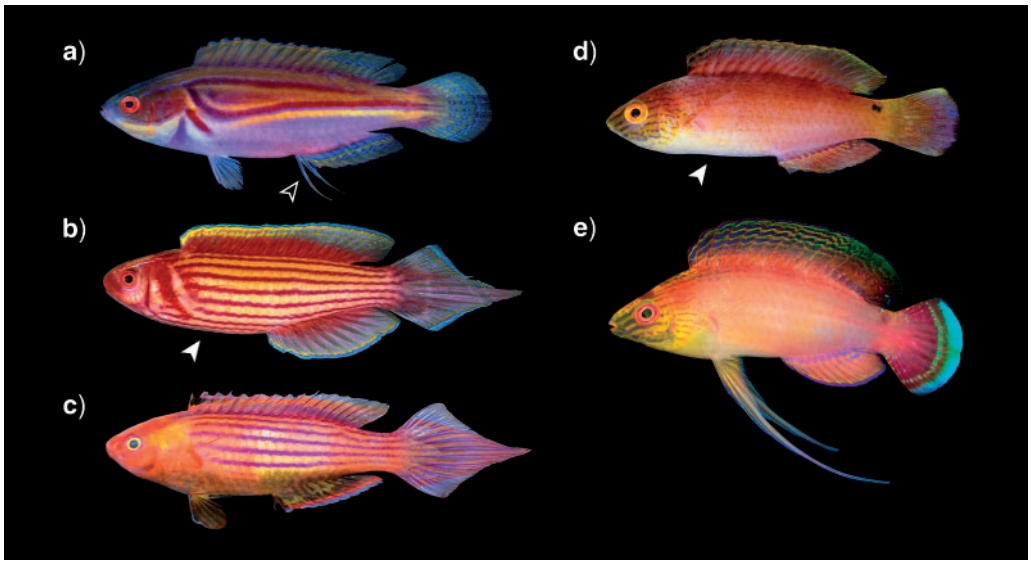

FIGURE 4. Selected species of fairy wrasses. a) *Cirrhilabrus laboutei*, USNM FIN 29549. Note the elongate anal-fin spines (open arrowhead). b) *Conniella apterygia*, USNM FIN 29616. Note the absence of pelvic fins (white arrow). c) *Cirrhilabrus earlei*. Note the general similarities in coloration and external morphology to *Conniella*. d) and e) *Cirrhilabrus pylei*. Note absence of pelvic fins (white arrowhead) in (d), a rare congenital defect in this otherwise fin-bearing species. Photographs by J. E. Randall, B. D. Greene, and Y. K. Tea.

Cirrhilabrus morrisoni, were absent in our data set. Similarly, *Cirrhilabrus johnsoni* from the *C. lunatus* complex, and *Cirrhilabrus randalli* and *Cirrhilabrus aurantidorsalis* from the *C. cyanopleura* complex were not sampled in our study.

Our maximum-likelihood and Bayesian phylogenomic analyses yielded disagreements in some inferred relationships within Lineage G, in particular the placement of the *C. condei* complex. One possible explanation is the limited representation of the *C. condei* complex, which includes three valid species, *Cirrhilabrus condei, Cirrhilabrus marinda*, and *Cirrhilabrus walshi*, of which the last two are rare and obtainable only with great logistical difficulty. Only *C. condei* was included in our analyses, and only on the basis of mitochondrial *COI*; we justify its inclusion in order to have representation of all species complexes.

Members of Lineage G are distinctive in having one row of cheek scales versus the usual two in all other species of *Cirrhilabrus.* This apomorphy was one of two characters justifying the erection of the genus *Cirrhilabrichthys* (for *C. filamentosus*) by Klausewitz (1976), with the other character being prolongation of the three posteriormost dorsal-fin spines into a single filament. Dorsal-fin prolongation is unusual in *Cirrhilabrus*, occurring almost exclusively within Lineage G, specifically the *C. filamentosus* and *C. rubriventralis* complexes (also independently acquired in *Cirrhilabrus nahackyi*).

Although dorsal-fin prolongation is not synapomorphic for either the *C. filamentosus* or *C. rubriventralis* complex, the occurrence of these characters at the complete exclusion of the *C. condei* complex suggests a sister relationship between the two on the basis of morphology (Tea et al. 2018a). Furthermore, the *C. rubriventralis* and *C. filamentosus* complexes have allopatric distributions in the Indian and Pacific Ocean basins, reflecting a common evolutionary history shared by many Indo-Pacific reef fishes (Randall 1988; Gaither and Rocha 2013; Liu et al. 2014; Ludt and Rocha 2014). Based on these additional lines of morphological and biogeographic evidence, we consider the relationships between these complexes inferred in our Bayesian analysis as having better support.

The placements of *C. claire, C. katoi*, and *C. laboutei* could not be previously resolved with confidence in analyses of mitochondrial *COI* (see Tea and Gill 2017; Tea et al. 2018b, 2020). Here, we place *C. claire* and *C. katoi* in the *C. lineatus* complex, but with coloration and morphological characters that depart from other members the group (see Tea et al. 2018b, 2020). The unusual *C. laboutei* occupies a monospecific lineage and is not found to be closely related to any of the extant species of *Cirrhilabrus*. On the basis of morphology, *C. laboutei* departs from all other species of *Cirrhilabrus* in possessing greatly elongate first and second anal-fin spines (Fig. 4a), a character that within the pseudocheilines is found only in the genus *Pseudocheilinus*.

Conniella apterygia: *The Mutant Wrasse*

We show in all analyses that *Conniella* is deeply nested within *Cirrhilabrus*. This enigmatic genus, with only one species (*Conniella apterygia* Allen 1983), was erected on the basis of lacking pelvic fins and associated osteology (Fig. 4b). In all other aspects of gross morphology, the genus is inseparable from *Cirrhilabrus* (Allen 1983). On the basis of coloration patterns, *Conniella*

shows a remarkable similarity to *Cirrhilabrus earlei* (Fig. 4c). Both species possess scales, along with several osseous elements, that retain and/or develop purple pigmentation even in preservation. This potentially plesiomorphic character is restricted to several species in the *C. jordani* complex (Tea et al. 2018b, 2019). Although these two species were not grouped together in any of our inferred trees, we note that some relationships within the complex were not confidently resolved, and that several species were not sampled for UCEs (including *C. earlei*).

The loss of pelvic fins and associated osteology is rare in percoid fishes (Yamanoue et al. 2010) and, within the Labridae, is reported in only one other species, *Siphonognathus argyrophanes* Cuvier 1829. Our phylogenomic analyses suggest that the loss of pelvic elements in *Conniella* is apomorphic. A parsimonious explanation is that this character was lost through genetic drift; in extreme endemics like *Conniella* with small effective population sizes, naturally occurring deleterious mutations can become fixed by chance (Price and Hadfield 2014; Sonsthagen et al. 2017). Indeed, fin loss has been reported in other species of *Cirrhilabrus* (Fig. 4d,e), indicating that loss of fins can occur naturally, albeit as a rare congenital defect. In order to preserve the monophyly of *Cirrhilabrus*, we recommend *Conniella* Allen 1983 be recognized as a junior synonym of *Cirrhilabrus*, Temminck and Schlegel 1845.

Evolutionary Timescale and Biogeographic History

Our dating analyses place the crown age of the pseudocheilines at 44.2 Ma (95% CI 33.4–51.4 Ma), an estimate that is concordant with those of several labrid studies using independent data sets (44.1 Ma [95% CI 36.9–51.4 Ma] in Cowman and Bellwood 2011; also see Alfaro et al. 2009). We note, however, that no study has previously included all component pseudocheiline genera, and that the different relationships inferred for the pseudocheilines by Cowman and Bellwood (2011) are likely to have been a result of incomplete sampling and missing data.

The fairy wrasses underwent a period of diversification that involved multiple invasions of the Indian Ocean. The genus has attained a geographic distribution spanning the entire Indo-Pacific, but with a disproportionate number of species occurring within the Coral Triangle. In contrast, species diversity decreases peripherally, with only eight species in the western Indian Ocean (including two species in the Red Sea), one species in Hawaii, and three species in the southeast Pacific Ocean. Our divergence-time estimates suggest the occurrence of two major periods of diversification: divergences among major *Cirrhilabrus* lineages during the late Miocene–Pliocene, followed by cladogenesis of species complexes during the Pliocene–Pleistocene. The former coincides with patterns of vicariance in other coral reef groups (including the Labridae) in the Indo-Pacific (4.1–7 Ma; Cowman and Bellwood 2013). For most of the *Cirrhilabrus* complexes, diversification occurred around the Pliocene–Pleistocene boundary, which marked the start of extensive glacial cycles (Ludt and Rocha 2014).

The combination of glacial cycles, the widespread dispersal capabilities of marine fishes (Quenouille et al. 2011; Gaither et al. 2015), and the permeability of ephemeral barriers on either side of the Indo-Australian Archipelago has led to shared faunal affinities, provincial endemism, and widespread distributions of species exhibited today, particularly for species in the central Indo-Pacific and Coral Triangle (Bellwood and Wainwright 2002; Connolly et al. 2003; Briggs 2005; Hobbs and Allen 2014; DiBattista et al. 2018, 2016). Our biogeographic analyses suggest that *Cirrhilabrus* and its major lineages originated in this region, in particular the central Indo-Pacific and Melanesia.

The Indian Ocean was colonized independently by five *Cirrhilabrus* complexes. Of these, only two are represented in peripheral regions of the western Indian Ocean (i.e., the Red Sea). Although the Red Sea began forming in the late Oligocene, environments conducive to coral reefs emerged only within the last 5 Myr (Siddall et al. 2003; Bosworth et al. 2005). Our temporal and biogeographic estimates for divergences of the Red Sea endemic *C. rubriventralis* (680 ka; 95% CI 20 ka–1.6 Ma) and *C. blatteus* (840 ka; 95% CI 11 ka–1.6 Ma) from their respective sister taxa are consistent with these dates, suggesting the possibility of dispersal from the western Indian Ocean.

The process of dispersal-mediated range expansion could also explain the regional endemism of the Hawaiian endemic *C. jordani*. Our biogeographic reconstruction placed the ancestor of *C. jordani* within several regions of the western Pacific Ocean, with southern Japan being the most likely ancestral area. The divergence of *C. jordani* from its sister lineage was estimated at 2.3 Ma (95% CI 1.1–3 Ma), which coincides with substantial lowering of sea levels in the Pleistocene. During this period, contemporary atolls would have been raised into table islands and exposed reefs, providing stepping-stones for the widespread dispersal of pelagic organisms (Kobayashi 2006; Eble et al. 2009). Colonization of Hawaii from southern Japan could have occurred via the numerous archipelagos connecting both regions, notably Midway Atoll (Randall et al. 1993). This region hosts a mixture of endemic Hawaiian and Japanese fauna, with recent studies suggesting that periodic connectivity occurred through to the last glacial cycle (see Tea et al. 2019). The alternative explanation for the occurrence of endemic species in peripheral regions is relictualism through extinction of intermediate populations. However, given the uneven distribution of *Cirrhilabrus* throughout its range and the recent evolutionary divergences for many species, isolation by dispersal appears to be a more parsimonious explanation.

The colonization history of the Indian Ocean is less clear for species in the *C. exquisitus* and *C. jordani* complexes. The former includes a single, highly polymorphic and widespread species spanning the entire range of the genus (but is curiously absent from

the Red Sea and Hawaii; Supplementary Fig. S4 available on Dryad). Our results suggest that divergence between the Indian and Pacific Ocean lineages of *C. exquisitus* occurred around 3.1 Ma (95% CI 1.6–5 Ma), during a period when fluctuating sea levels are likely to have cut off exchange between the eastern Indian Ocean and the Indo-Australian Archipelago (Ludt and Rocha 2014). This distinction between the Indian and Pacific Ocean lineages of *C. exquisitus* is supported by both UCE data and mitochondrial *COI* (Supplementary Fig. S4 available on Dryad). However, due to the lack of samples from the eastern Indian Ocean and other regions of the Pacific Ocean, we were unable to confidently determine the ancestral area of origin for this species complex, nor infer the processes leading to diversification within the two major lineages in each ocean basin.

Identifying the biogeographic drivers of speciation for other *Cirrhilabrus* complexes remains problematic, particularly in the *C. cyanopleura* complex, where contemporary distribution patterns include extensive sympatry between species. While evidence from both empirical and theoretical studies indicates the possibility of sympatric speciation on coral reefs, the process remains contentious (Rocha and Bowen 2008). Our results explain the tight clustering of *Cirrhilabrus* species within the Coral Triangle through late Miocene diversification of major lineages, followed by extensive cladogenesis of species complexes during the late Pliocene to Pleistocene. While this period was characterized by glacial cycles that promoted diversification in coral reef fishes, the formation of barriers was often ephemeral across short spatial and temporal scales (particularly around the Indo-Australian Archipelago; Rocha and Bowen 2008), with few opportunities for prolonged and continuous dispersal into wider, more peripheral regions. In short, the repeated fluctuations of sea levels during the late Pliocene–Pleistocene might have acted as a species pump, leading to diversification on a localized scale through episodic barrier formation, but with few opportunities for more widespread colonization.

Conclusions

Our study demonstrates both the capacity and limitations of genome-wide UCEs in resolving phylogenetic relationships in a recently diverged group characterized by few robust morphological characters. We show that a summary-coalescent approach is unable to resolve the evolutionary relationships of *Cirrhilabrus*, probably because of poorly resolved gene trees. In contrast, analysis of concatenated sequence data appears to resolve the relationships among species even across shallow timescales, but we cannot rule out errors due to introgression or incomplete lineage sorting. Importantly, our investigation highlights the importance of scrutinizing the information content of loci used in phylogenomic analyses.

Our phylogenomic analyses of the fairy wrasses have provided novel insights into the evolutionary history, timing of divergences, and historical biogeography of one of the largest and most charismatic genera of labrid fishes. Although the emergence of the fairy wrasses coincided with patterns of Miocene vicariance typical of other groups of coral reef fishes, much of their diversification took place in the Pliocene–Pleistocene. Further investigation with an expanded data set will provide additional insights into the extent of incomplete lineage sorting and introgression among the fairy wrasses, leading to a more confident resolution of their evolutionary history.

Supplementary Material

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4tmpg4f6q.

Funding

This work was funded by a Research Training Program Scholarship from the Australian Government and by an Australian Museum Research Institute Postgraduate Award to Y.K.T.; the Australian Research Council [FT160100463 and FT160100167 to N.L. and S.Y.W.H.]; and an ARC DECRA Fellowship [DE170100516] and the ARC Centre of Excellence Program [CE140100020] to P.F.C.

Acknowledgments

We thank Amanda Hay, Sally Reader, and Kerryn Parkinson of the Australian Museum for curatorial support. Gerald R. Allen (Western Australian Museum), David R. Bellwood (James Cook University), Michael P. Hammer (Museum and Art Gallery of the Northern Territory), Luiz A. Rocha (California Academy of Sciences), Kelvin Lim (Lee Kong Chian Natural History Museum), Benjamin C. Victor, and Fenton Walsh provided valuable tissue samples. All genetic materials obtained from museums were procured in accordance with guidelines and approval from the respective institutions. Tissue curation and DNA extractions were performed by Martina de Freitas Prazeres, Hillary Smith, and Julia Yun-Hsuan Hung. Benjamin W. Frable and Joseph Rowlett provided valuable discourse on the subject matter. Charles P. Foster and Kevin Love provided custom scripts for data handling. We dedicate this study to the late John Ernest Randall, who was a fierce and pioneering force in the modern age of ichthyology, and to Hiroyuki Tanaka, who has contributed significantly towards our understanding of the genus. The paper benefited from comments by Bryan Carstens, Rayna Bell, Prosanta Chakrabarty, and four anonymous reviewers.

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