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Dating the evolutionary origins of coral reef fishes

Thesis submitted by

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for the degree of Doctor of Philosophy in Marine Biology

within the School of Marine and Tropical Biology and

the ARC Centre of Excellence for Coral Reef Studies,

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Statement on the Contribution of Others

This thesis includes some collaborative work with my supervisors Prof. David Bellwood, and Dr. Lynne van Herwerden. While undertaking these collaborations, I was responsible for the project concept and design, data collection, analysis and interpretation, and the final synthesis of results into a form suitable for publication. My collaborators provided intellectual guidance, equipment, financial support, and editorial assistance.

A chapter of this thesis forms a collaborative publication with my supervisors (roles in parentheses) DR Bellwood (initial project design, tissue samples), L van Herwerden (initial analyses); and three other colleagues: Dr. Selma Klanten (sequencing and initial analyses), Dr. Morgan Pratchett (ecological data) and Dr. Nicolai Konow (tissue samples). All authors contributed to earlier drafts of the paper. While I was not lead author, my contribution to the project was substantial and the topic and results are pertinent to my thesis subject. My contribution to the project is outlined below and all co-authors support its inclusion in this body of work (see Consent of co-authors).

Financial support for the project was provided by James Cook University Graduate Research Scheme and the Australian Research Council Centre of Excellence for Coral Reef Studies. Tuition support was provided by the Endeavour International Postgraduate Research Scholarship and stipend support was provided by a James Cook University Postgraduate Research Scholarship. Financial support for conference travel was provided by the Australian Research Council Centre of Excellence for Coral Reef Studies, the Australian Coral Reef Society, and the Australian National Network in Marine Science (ANNiMS).

Consent of Co-authors:

Details of Chapter and associated publication	Nature and extent of Candidate's intellectual input	I confirm the candidate's contribution and consent to the inclusion of the paper in this thesis
<p style="text-align: center;">Chapter 3:</p> <p style="text-align: center;">Evolutionary origins of the butterflyfishes (f. Chaetodontidae) and the rise of corallivory on reefs.</p> <p style="text-align: center;">Publication:</p> <p>Bellwood DR, Klanten S, Cowman PF, Pratchett MS, Konow N, van Herwerden L (2010) Evolutionary history of the butterflyfishes (f. Chaetodontidae) and the rise of coral feeding fishes. J Evol Biol 23: 335-349</p>	<ul style="list-style-type: none"> • Age estimating procedures using BEAST package with aligned sequence data. • Post-analysis assessment of BEAST results files and chronogram construction. • Optimisation of habitat and feeding preference on chronology • Diversification rate analysis using R framework • Assessment of variation of rate of cladogenesis through time • Use of GEIGER package to identify significantly more diverse clades within family • Writing preparation of methods sections: <i>Molecular dating; Optimising ecological traits; Diversification Statistics</i> and corresponding Results section. • Major contributions to writing of Introduction, Discussion, and editing of manuscript • Preparation of Table 1, Fig. 2; and Appendix S2, Fig. S1 and S2 	<p>Name: Prof. David Bellwood</p> <p>Signature:</p>
		<p>Name: Dr. Lynne van Herwerden</p> <p>Signature:</p>
		<p>Name: Dr. Selma Klanten</p> <p>Signature:</p>
		<p>Name: Dr. Morgan Pratchett</p> <p>Signature:</p>
		<p>Name: Dr. Nicolai Konow</p> <p>Signature:</p>

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Abstract

This thesis examines the origins and maintenance of the high diversity of coral reef fishes in the Indo-Australian Archipelago (IAA), the largest marine biodiversity hotspot. Bayesian age estimation techniques, combining molecular and palaeontological data, were used to reconstruct an evolutionary timeline for four conspicuous coral reef fish families: the Labridae (wrasses), Chaetodontidae (butterflyfishes), Pomacentridae (damselfishes) and Apogonidae (cardinalfishes). First, the evolutionary origins of trophic novelty and habitat preference were explored in the Labridae and Chaetodontidae. Then, to assess congruence in patterns of cladogenesis, rates of diversification and lineage accumulation were compared for the four families. Finally, to gain a biogeographic perspective, ancestral range reconstruction was used to compare global patterns of origination and dispersal. Specifically, the origins and progression of biodiversity in the IAA was compared to other marine provinces. Combined, these data provided an insight into the evolution of this complex association between fishes and coral reefs.

A chronogram of the Labridae identified molecular origins in the late Cretaceous, with both major lineages (hypsignyine and julidine) present shortly after the K/T boundary (~63 MY). All major lineages were in place by the beginning of the Miocene (23 MY) with most diversification in extant lineages occurring within the Miocene. Multiple origins of novel feeding modes were revealed with two distinct pulses. The Palaeocene/Eocene saw the origins of feeding modes that are well represented in other families: gastropod feeders, piscivores and browsing herbivores. A second wave of innovation in the Oligocene/Miocene resulted in more specialised feeding modes: coral feeding, foraminifera feeding and fish cleaning.

There is little evidence of a general relationship between trophic specialisation and species diversity. All major feeding modes on present day reefs were probably already in place 7.5 million years ago.

The Chaetodontidae stem lineage has origins in the Eocene and by the early Oligocene the two major lineages have diverged: bannerfishes and butterflyfishes. Optimisation of recent ecological data reveal that corallivory has arisen at least five times over a period of 12 MY, from 15.7 to 3 MY. Significantly higher diversity was recorded in lineages of the genus *Chaetodon*, in which the greatest number of corallivores are found. However, it was the move onto coral reefs in the Miocene, not corallivory that foreshadowed rapid cladogenesis within *Chaetodon*. This coincides with a global reorganisation of coral reefs and the expansion of fast-growing corals. This historical association underpins the sensitivity of specific butterflyfish clades to global coral decline.

Previous chronologies of the Labridae and Chaetodontidae were reassessed with increased taxon sampling, and added fossil data. For the first time, the timing of diversification within the Pomacentridae and Apogonidae were estimated using Bayesian inference. Lineage through time plots for these four families revealed a possible late Eocene/early Oligocene cryptic extinction event coinciding with the collapse of the ancestral Tethyan/Arabian hotspot. Rates of diversification analysis revealed elevated cladogenesis in all four families in the Oligocene/Miocene. In this rebound, lineages with a high percentage of coral reef associated taxa display significantly higher diversities and higher net diversification rates than expected, throughout the Miocene epoch. Similar patterns were found in other reef associated fish and gastropod groups. The development of a complex mosaic of reef habitats in the IAA during the Oligocene/Miocene period appears to have been a significant

driver of cladogenesis at this time. Patterns of diversification among taxa suggest that coral reefs also acted as a refuge from high extinction, as reef taxa are able to sustain significant diversity at higher extinction rates than their non-reef counterparts. As such, the IAA appears to support both cladogenesis and survival in associated lineages, laying the foundation for the Recent IAA marine biodiversity hotspot.

Ancestral range reconstruction of the Chaetodontidae, Pomacentridae and Labridae revealed temporal patterns of origination and dispersal between the East Pacific, Atlantic, Indian Ocean, IAA and Central Pacific. The IAA acts as both a centre of origination and as a source of diversity to the Indian Ocean and Central Pacific, for all three families. The Atlantic and East Pacific both show high relative rates of origination, however, on a global scale these regions support significantly lower origination than the IAA. Inferred palaeodiversity of ancestral lineages is masked by the extinction of lineages following the closure of the Tethys seaway and decline of ancestral biodiversity hotspots. Lineages of Eocene and Oligocene origin that appear restricted to the IAA would have been peripheral at the time to the Tethyan hotspot. However, it was the proliferation and expansion of these restricted lineages throughout the Miocene that underpins the diversity in the IAA hotspot and across the entire Indo-Pacific. The distribution of vicariance events across known historical barriers highlights the lack of temporal congruence among taxa in the Isthmus of Panama, the East Pacific Barrier and the Terminal Tethyan Event, but much greater congruence between the IAA, Indian and Pacific Oceans.

In summary, for three of the four families, initial divergences following the K/T boundary represent the origins of generalised feeding strategies. During this time there was the potential for panmixia between all ocean regions. The apparent slowdown in net speciation rate throughout the Eocene may reflect a late

Eocene/Oligocene cryptic extinction event. The survival and subsequent proliferation of Eocene lineages restricted to the IAA during the Miocene underpins much of the current biodiversity on coral reefs and laid the foundation for a wave of trophic innovation in the Labridae and Chaetodontidae. In all four families, Recent patterns are a result of evolutionary, geological and ecological factors spanning over 40 to 60 MY. Today's hotspot is the product of long history of division, decline and diversification.

Table of Contents

	Page
Statement on the Contribution of Others	i
Consent of Co-authors:	ii
Acknowledgements	iii
Abstract	v
Table of Contents	ix
List of Figures	xi
List of Tables	xiii
Chapter 1: General Introduction	1
Chapter 2: Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs	9
<i>Published in Molecular Phylogenetics and Evolution 52:621-631</i>	
2.1. Introduction	9
2.2. Materials and Methods	12
2.3. Results	20
2.4. Discussion	28
2.5. Conclusions	37
Chapter 3: Evolutionary history of the butterflyfishes (f: Chaetodontidae) and the rise of coral feeding fishes	38
<i>Published in Journal of Evolutionary Biology 23:335-349</i>	
3.1. Introduction	38
3.2. Materials and Methods	42
3.3. Results	49
3.4. Discussion	58
3.5 Conclusions	68
Chapter 4: Coral reefs as drivers of cladogenesis in teleost fishes: expanding coral reefs, cryptic extinction events and the development of biodiversity hotspots	69
<i>Published in Journal of Evolutionary Biology 24:2543-2562</i>	
4.1 Introduction	69

4.2. Materials and Methods	73
4.3. Results	85
4.4. Discussion	108
4.5. Conclusions	121
Chapter 5: Patterns of origination and dispersal: historical biogeography of teleosts on coral reefs	123
<i>In prep for publication in Journal of Biogeography</i>	
5.1. Introduction	123
5.2. Materials and Methods	129
5.3. Results	136
5.4. Discussion	153
5.5 Conclusion	176
Chapter 6: Concluding Discussion	177
Appendix A: Supplementary information for Chapter 2	217
Appendix B: Supplementary information for Chapter 3	225
Appendix C: Supplementary information for Chapter 4	235
Appendix D: Supplementary information for Chapter 5	253
Appendix E: Publications arising from thesis	266

List of Figures

	Page
Figure 2.1 A phylogeny representing best ML topology tree of the Labridae from 10 individual runs in Garli.	21
Figure 2.2 A chronogram illustrating the ages of origin and diversification of the Labridae.	24
Figure 2.3 Origins of novel feeding modes throughout the evolutionary history of the Labridae.	26
Figure 2.4 Biplot of the relationship between species richness, lineage age and trophic specialisation.	27
Figure 3.1 Inferred phylogeny of the family Chaetodontidae, obtained by Bayesian, maximum parsimony and maximum likelihood analyses for three loci.	52
Figure 3.2 A chronogram of the Chaetodontidae with optimised trophic modes reveals five independent origins of corallivory over the last 8.4 - 2.1 MY.	55
Figure 4.1 Chronograms reconstructed from three independent BEAST MCMC analyses illustrating major lineages for (A) the Labridae, and (B) the Chaetodontidae.	90
Figure 4.2 Chronograms reconstructed from three independent BEAST MCMC analyses illustrating major lineages for (A) the Apogonidae, and (B) the Pomacentridae.	91
Figure 4.3 (A) Lineage through time plot for each of the four families. (B) Variation over time in the numbers of fossil marine organisms. (C) Line graph showing origins of other reef and coastal groups with circles representing significantly more diverse lineages.	104
Figure 4.4 Independent LTT plots for the Labridae, Pomacentridae, Apogonidae, and Chaetodontidae.	105
Figure 4.5 (A) Relationship between coral reef association and diversification rate among families. (B) Relationship between lineages with a significantly higher diversity at a given rate of extinction and extent of coral reef association (% taxa living on reefs).	107

Figure 4.6 Schematic diagram representing the relationship between fossil diversity, and LTT plot of an ultrametric phylogeny (cf. Crisp and Cook 2009).	113
Figure 5.1 Schematic drawing of global marine biogeographic regions and how they have changed from the Palaeocene/Eocene to the Pliocene/Recent epochs.	132
Figure 5.2 Hypothetical range reconstruction scenarios implement in Lagrange (Ree and Smith 2008).	133
Figure 5.3 Boxplot showing mean (circle) and 95% CI (whiskers) of the distribution of ages of origination of extant species in each biogeographic region, and globally for the Labridae, Pomacentridae, Chaetodontidae.	139
Figure 5.4 (A) Schematic drawing of globe displaying combined diversity of labrids, pomacentrids and chaetodontids in each region. (B) Bar graph of mean relative proportion of lineage origination in each region, per capita regional diversity. (C) Bar graph of mean relative proportion of lineage origination in each region, per capita family diversity.	142
Figure 5.5 Schematic drawing of global palaeomaps for four time periods showing palaeodiversity, origination and dispersal in each period for the Labridae and Pomacentridae.	147
Figure 5.6 Schematic drawing of global palaeomaps for four time periods showing palaeodiversity, origination and dispersal in each period for the Chaetodontidae.	148
Figure 5.7 Frequency histogram of vicariance events across all barriers in all three families.	151
Figure 5.8 Distribution of reconstructed vicariance events associated with barriers between biogeographic region (see, Fig. S5.2-5.4 Appendix D).	152

List of Tables

	Page
Table 2.1 Uniform and parametric priors, and fossil/biogeographic evidence used for calibration points on chronogram representing the most recent common ancestor (MRCA) of certain labrid genera.	18
Table 2.2 Age estimates from Bayesian inference in BEAST for initial divergence and subsequent diversification of labrid groups.	19
Table 3.1 Departure of chaetodontid lineages from global diversification rate estimated of the family Chaetodontidae.	57
Table 4.1 Fossil and biogeographic age constraints and their sources used for age estimation in BEAST for the families Labridae, Chaetodontidae, Pomacentridae and Apogonidae.	76
Table 4.2 Gamma statistic values from CR test and MCCR adjusted p-values for each family.	78
Table 4.3 Departure of lineages from the global rate of diversification for each family.	95
Table 4.4 MEDUSA results ranking rate shift models based on Δ AIC score for the families Labridae, Chaetodontidae, Pomacentridae and Apogonidae.	100
Table 4.5 Ranking of diversification models fit to branching time from BEAST generated chronograms using Δ AIC and AIC weight (w_{AIC}).	101
Table 5.1 Assignment of locations within species ranges to five biogeographic regions to be used in ancestral range reconstruction.	131
Table 5.2 Results from Lagrange ancestral range reconstruction under three models.	137
Table 5.3 Relative contribution of origination (Origin), dispersal (Disp.) and inheritance (Inh) per capita regional biodiversity of the Labridae, Pomacentridae, and Chaetodontidae.	141

