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Relationships of the temperate Australasian labrid fish tribe Odacini (Perciformes; Teleostei)

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Abstract

The labrid tribe Odacini comprises four genera and 12 species of fishes that inhabit shallow kelp forest and seagrass areas in temperate waters of Australia and New Zealand. Odacines are morphologically disparate, but share synapomorphies in fin structure and fusion of teeth into a beak-like oral jaw. A phylogenetic analysis of odacines was conducted to investigate their relationships to other labrid fishes, the relationships of species within the tribe, and the evolution of herbivory within the group. Fragments from two mitochondrial genes, 12S rDNA and 16S rDNA, and two nuclear genes, Tmo4C4 and RAG2, were sequenced for seven odacine species (representing all four genera), eight species representing the other major labrid lineages, and three outgroup species. Maximum likelihood and maximum parsimony analyses on the resulting 2338 bp of DNA sequence produced nearly identical topologies differing only in the placement of a clade containing the cheiline *Cheilinus fasciatus* and the scarine *Cryptotomus roseus*. The remaining clades received strong bootstrap support under maximum parsimony, and all clades in the maximum likelihood analysis received high bootstrap proportions and high posterior probabilities. The hypsigenyine labrid *Choerodon anchorago* formed the sister group to the odacines. Within the odacines, *Odax cyanoallix* + *Odax pullus* formed the sister to the remaining odacines, with *Odax acroptilus*, *Odax cyanomelas*, and *Siphonognathus argyrophanes* forming successively closer sister groups to the clade *Haletta semifasciatus* + *Neoodax balteatus*. Either herbivory evolved twice in the odacines, or herbivory evolved once with two reversions to carnivory. The latter hypothesis appears more likely in the light of odacine feeding biology.

1. Introduction

Perciform fishes of the suborder Labroidei are an ecologically important group that are highly characteristic of reef environments (Choat and Bellwood, 1991). They display high levels of species diversity, a number of distinctive and novel feeding modes, and share similarities in feeding structures especially in the pharyngeal jaws (Liem and Greenwood, 1981). Despite the importance of these fishes, relationships within the Labroidei have not been well resolved and remain controversial (Johnson, 1993; Streelman and Karl, 1997).

Liem and Greenwood (1981) demonstrated that the marine labroid families Labridae (wrasses), Scaridae (parrotfishes), and Odacidae (butterfishes or weed whitings) shared derived features of the pharyngeal apparatus, and thus formed a monophyletic assemblage. Kaufman and Liem (1982) then suggested that this clade should be recognized as a single family Labridae, which has since been divided into ten tribes including the scarines and odacines (Gomon, 1997; Hanel et al., 2002; Russell, 1988). Despite recent interest in relationships within several of these labrid tribes (e.g. Bernardi et al., 2000; Gomon, 1997; Hanel et al., 2002; Parenti and Randall, 2000; Russell, 1988; Streelman et al., 2002; Westneat, 1993), there has been little attempt to elaborate relationships between them. As a result, the evolutionary origins of the ecologically divergent odacines and scarines among the labrids remain unclear.

The tribe Odacini with 12 species restricted to temperate waters of Australia and New Zealand is depau-

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perate in the context of the Labridae with 553 species worldwide (Parenti and Randall, 2000). The odacines have many typical labrid characters (Russell, 1988), but share several synapomorphies including fusion of the jaw teeth into a beak (Gomon and Paxton, 1985). Odacines are highly disparate in both morphology and ecology (Gomon and Paxton, 1985), inhabiting both reef and seagrass areas and feeding on a range of prey including benthic invertebrates, detritus and kelps (Choat and Clements, 1992; Clements and Choat, 1993; Edgar and Shaw, 1995; MacArthur and Hyndes, 2001). Indeed, three species of the genus *Odax* are highly unusual among temperate-water fishes and unique among labrids in their selective diet of fucoid and laminarian macroalgae and their use of hindgut fermentation (Ayling and Paxton, 1983; Clements et al., 1994; Mountfort et al., 2002). The only other herbivorous labrids, the scarines, are restricted to tropical areas (Streelman et al., 2002) and have low levels of fermentation products in the gut (Clements and Choat, 1995).

The unique nature of herbivory in the odacines raises the interesting question of its evolutionary origin. The odacines lack a fossil record, and so placing odacine herbivory in an historical context requires an understanding of their systematic relationships. Gomon and Paxton (1985) revised the group on the basis of external and osteological characters, and advocated the recognition of four genera. The monotypic *Neoodax* (*N. balteatus*) and *Haletta* (*H. semifasciata*) are restricted to Australia, as is *Siphonognathus* with six species (*S. argyrophanes, S. attenuatus, S. beddomei, S. caninus, S. radiatus*, and *S. tanyourus*) (Gomon and Paxton, 1985). The genus *Odax* includes two Australian species (*O. acroptilus* and *O. cyanomelas*) and two New Zealand species (*O. cyanoallix* and *O. pullus*). While Gomon and Paxton (1985) defined these four genera on the basis of proposed morphological synapomorphies, they noted that the extreme morphological disparity displayed by the odacines made generic boundaries somewhat arbitrary.

Beyond defining four genera, Gomon and Paxton (1985) hypothesized the following relationships among the odacines: (i) the *Odax* species fell into two pairs of sister taxa, one in New Zealand and one in Australia; (ii) *Neoodax balteatus* was the sister group to the remaining odacine species due to its generalized characters and resemblance to an unspecialized julidine labrid; (iii) *S. radiatus* was the sister group to the remaining *Siphonognathus* species, and (iv) *S. beddomei* and *S. argyrophanes* were sister taxa. Gomon and Paxton did not include a consideration of the labrid sister taxon to the odacines, although more recently both Russell (1988) and Gomon (1997) advocated inclusion of the monotypic labrid genus *Cheilio* within the Odacini on the basis of similarities in external morphology. *Cheilio inermis* has a wide tropical Indo-Pacific distribution, and although found on coral reefs mainly occurs in habitats dominated by seagrass or macroalgae (Randall et al., 1997).

We sought to examine the evolutionary history of odacines further by examining their ecology and morphology in the context of a molecular phylogeny constructed from mitochondrial and nuclear DNA sequences. We asked three specific questions: (i) What is the evolutionary position of the odacines within the Labridae?; (ii) Is *Cheilio inermis* the sister taxon to a monophyletic Odacini?; and (iii) What is the evolutionary pattern of herbivory within the Odacini? Clearly, resolving these questions will also shed light on the broader issue of evolutionary relationships within the Labridae as a whole.

2. Materials and methods

2.1. Selection of ingroup and outgroup taxa

The samples used in this study represent 16 genera and 19 species of labroid fishes, and are presented in Table 1. The ingroup taxa comprised eight species of odacines *sensu* Russell (1988) and Gomon (1997), including representatives of all five genera (*Cheilio*, *Haletta*, *Neoodax*, *Odax*, and *Siphonognathus*). We included all four species of the genus *Odax* to allow an examination of herbivory within the odacines. To polarize characters within the Labridae, and potentially to allow odacines to fall outside the Labridae, we included three non-labrid labroid outgroups: the cichlid *Thorichthys meeki*, the embiotocid *Amphisticus argenteus* and the pomacentrid *Abudefduf saxatilis*. Since the hypsigenyines have been suggested as the sister group to the remainder of the Labridae (Bellwood, 1994), we included representative of three hypsigenyine genera (*Bodianus, Choerodon* and *Lachnolaimus*). To test for possible relationships between odacines and other labrid tribes, including several that have been suggested as being closely related to odacines, we included representatives of four additional labrid tribes. These were the scarines (*Cryptotomus*), the temperate Southern Hemisphere pseudolabrines (*Notolabrus*), the cheilines (*Cheilinus*), and two members of the julidine lineage (*Halichoeres* and *Coris*).

Collection locations and tissue catalog numbers for specimens are presented in Table 1. Fishes were collected from the wild (except for the cichlid *Thorichthys meeki*) by spear, net or rotenone. At site of capture muscle samples were frozen in liquid nitrogen or placed in 70% ethanol.

2.2. DNA extraction

Genomic DNA was extracted from approximately 2 to 4 mm^3 of tissue sample using a Puregene DNA isolation kit (Gentra Systems, Minneapolis, MN). Briefly,

Table 1
List of labroid species used in this study, following accepted classification (Gomon, 1997), collecting locations, tissue catalog numbers and GenBank Accession numbers

Taxon	Collecting location	Tissue catalog number	GenBank Accession number			
			12S	16S	Tmo4C4	RAG2
Family Cichlidae						
Thorichthys meeki	Aquarium trade	FMNH MW00-10	AY279566	AY279669	AY279772	AY279875
Family Embiotocidae						
Amphisticus argenteus	California, USA	KU KM505	AY279571	AY279674	AY279777	AY279880
Family Pomacentridae						
Abudefduf saxatilis	Belize	FMNH BZ99-24	AY279570	AY279673	AY279776	AY279879
Family Labridae						
Tribe Cheilini						
Cheilinus fasciatus	Great Barrier Reef, Australia	FMNH MW93-3	AY279580	AY279683	AY279786	AY279889
Tribe Hypsigenyini						
Bodianus mesothorax	Thailand	FMNH MW94-14	AY279578	AY279681	AY279784	AY279887
Choerodon anchorago	Philippines	FMNH MW95-55	AY279585	AY279688	AY279791	AY279894
Lachnolaimus maximus	Belize	FMNH BZ99-8	AY279618	AY279721	AY279824	AY279927
Tribe Julidini						
Halichoeres hortulanus	Solomon Islands	FMNH SOL98-22	AY279601	AY279704	AY279807	AY279910
Coris aygula	Great Barrier Reef, Australia	FMNH FNQ93-62	AY279589	AY279692	AY279795	AY279898
Tribe Odacini						
Cheilio inermis	Philippines	FMNH MW95-83	AY279583	AY279686	AY279789	AY279892
Haletta semifasciata	Victoria, Australia	NMV NMV-a22829a	AY279656	AY279759	AY279862	AY279965
Neoodax balteatus	Victoria, Australia	NMV NMV-a22828a	AY279657	AY279760	AY279863	AY279966
Odax acroptilus	Sydney, Australia	FMNH FNQ93-21	AY279658	AY279761	AY279864	AY279967
O. cyanoallix	Three Kings Islands, NZ	K. Clements 2/3/93-1	AY279660	AY279763	AY279866	AY279969
O. cyanomelas	Sydney, Australia	AMS I.38734041-a	AY279661	AY279764	AY279867	AY279970
O. pullus	Chetwode Islands, NZ	K. Clements 10/7/01-2	AY279659	AY279762	AY279865	AY279968
Siphonognathus argyrophanes	Moonta Bay, South Australia	SAM SAMAF9353	AY279662	AY279765	AY279868	AY279971
Tribe Pseudolabrini						
Notolabrus gymnogenis	Sydney, Australia	FMNH MW93-19	AY279625	AY279728	AY279831	AY279934
Tribe Scarini						
Cryptotomus roseus	Belize	T. Streelman 98-CR2	AY279592	AY279695	AY279798	AY279901

tissue was homogenized in a low molarity salt buffer and digested overnight with proteinase K (Davis et al., 1986). DNA was then precipitated in 100% isopropanol with 20 mg ml^{-1} glycogen at room temperature. We pelleted the DNA by centrifugation on high speed followed by washing in 70% ethanol. DNA was then stored at 4 °C in Puregene DNA hydration solution.

2.3. PCR amplification

Aliquots of genomic DNA isolates were used as templates for polymerase chain reaction (PCR) to amplify double-stranded DNA products from two mitochondrial genes, 16S rDNA (Kocher et al., 1989) and 12S rDNA, and two nuclear genes, Tmo4C4 (Streelman and Karl, 1997) and RAG2 (Lovejoy, 1999; Sullivan et al., 2000). Each PCR had a reaction volume of 25 μl and contained 1 μl DNA stock regardless of stock concentration (diluted 1:10 in some cases), 2.5 μl of 10× reaction buffer (100 mM Tris–HCl, 500 mM KCl, 15 mM $MgCl_2$, pH 8.3; Roche, Mannheim, Germany), 1.5 μl of 8 mM premixed deoxynucleotide triphosphates, 0.1 μl of 5 U ml^{-1} *Taq* polymerase (Roche, Mannheim, Germany), and 1 μl of each oligonucleotide primer, each at 10 μM concentration. Primers used for amplification and sequencing are given in Table 2. Some samples amplified weakly using standard PCR, and were reamplified using Ready-to-go PCR beads (Amersham–Pharmacia Biotech, Piscataway, NJ).

Each 12S and 16S PCR included an initial denaturation step at 94 °C for 2 min, followed by 30 cycles of PCR. The cycles for 12S involved denaturation at 94 °C for 30 s, annealing at 60 °C for 30 s, and extension at 72 °C for 55 s. The cycles for 16S were the same as for 12S except the annealing temperature was at 49 °C. After a final extension step at 72 °C for 2 min the PCR products were held at 4 °C. Each RAG2 and Tmo4C4 PCR included an initial denaturation step at 95 °C for 1 min, followed by 36 cycles of PCR. The cycles involved denaturation at 95 °C for 30 s, annealing at 55 °C for 1 min, and extension at 72 °C for 90 s. The final extension step was at 72 °C for 5 min. PCRs were performed using an MJ Research PTC-200 Peltier Thermal Cycler (MJ Research, Watertown, Mass.).

All PCR products were loaded and run on agarose gels, then bands were cut out, melted at 70 °C, and incubated in GELase Agarose Gel-Digesting Preparation (Epicentre, Madison, WI) for at least 3 h at 45 °C. PCR products (0.7 μl) were cycle-sequenced using an ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit, version 1.0 (Applied Biosystems, Foster City, CA). The cycling protocol used involved 32 cycles of denaturation at 96 °C for 30 s, annealing at 50 °C for 15 s, and extension at 60 °C for 4 min. Sequences of both strands were generated on an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA) using the amplification primers.

2.4. Sequence alignment

Sequences from all genes were trimmed to the size of the smallest fragment to minimize the amount of missing data that was introduced to the data matrix. RAG2 and Tmo4C4 sequences were aligned by eye using Sequencher 3.0 (Gene Codes Corp). 16S sequences were aligned to previously published secondary structure models for teleosts (Ortí and Meyer, 1997) using the data editor in PAUP*4.0b8 (Swofford, 2000). 12S sequences were

Table 2
Primers and primer sequences used for amplification and sequencing in this study

Gene	Primer name	Primer sequence
12S rDNA	12s53F	CAC AAA GGC TTG GTC CTG ACT TT
	12s489F	CTG GGA TTA GAT ACC CCA CTA TGC
	12s613R	TCG GTT CTA GAA CAG GCT CCT CTA G
	12s991R	GGT ACA CTT ACC ATG TTA CGA CT
16S rDNA	16SAR	CGC CTG TTT ATC AAA AAC AT
	16SBR	CCG GTC TGA ACT CAG ATC ACG T
Tmo4C4	Tmo-f1-5	CCT CCG GCC TTC CTA AAA CCT CTC
	Tmo-f1-6[a]	GAA AAG AGT GTT TGA AAA TGA
	Tmo-r1-3	CAT CGT GCT CCT GGG TGA CAA AGT
RAG2	Andy-f[b]	CTG GCC AAA ACG CTC ATG TCC AAC
	RAG2-f1	GAG GGC CAT CTC CTT CTC CAA
	Isben-f[c]	TGG AAC AGT GTM RTT GAC TGT CC
	RAG2-f2	GAC TGT CCT CCT CAG GTG TTC
	RAG2-r2	GTC TGT AGA GTC TCA CAG GAG AGC A
	Fisk-r[b]	CCA CCA AAC CAT GTA CGA CTA TGG
	RAG2-r3	GAT GGC CTT CCC TCT GTG GGT AC
	JohnD-r[c]	GTG GAC TCC TGG CTG CAK CCC TG

[a] *Notolabrus gymnogenis.*
[b] *Siphonognathus argyrophanes.*
[c] *Haletta semifasciata, Neoodax balteatus* (one individual).

aligned to a secondary structure for labrids (Alfaro and Westneat, unpublished data) based on mammalian models (Gutell, 1994; Springer and Douzery, 1996). For both ribosomal genes, ambiguously alignable regions, usually corresponding to loops, were excluded from further analysis. After excluding unalignable regions and trimming sequence ends the RAG2 gene partition contained 775 characters, the Tmo4C4 partition contained 443 characters, the 16S partition contained 377 characters, and the 12S partition contained 743 characters for a total of 2338 nucleotide characters. All sequences were deposited in GenBank (Table 1).

2.5. Phylogenetic analyses

2.5.1. Congruence evaluation

The conditions under which data sets can be appropriately combined has been the subject of considerable controversy (see Bull et al., 1993). The partition homogeneity test is one approach to specifying these conditions, however recent studies have suggested that this test may be sensitive to both the number of characters and levels of homoplasy among partitions (Dolphin et al., 2000; Dowton and Austin, 2002). We assessed incongruence among the four gene partitions (12S, 16S, RAG2, and Tmo4C4) in two ways: with the partition homogeneity test and by comparing bootstrap trees from each partition. We performed pairwise partition homogeneity tests in PAUP, using the heuristic search option with two random addition sequence replicates and 1000 total replicates to generate the null distribution for the test. Following Cunningham (1997) we adopted a significance level of 0.01 and excluded invariant sites. We bootstrapped individual gene partitions 1000 times using the heuristic search option and two random addition sequence replicates.

2.5.2. Tree construction

Phylogenetic analyses were conducted using a beta version of PAUP* (4.0b10). Heuristic searches to find the most parsimonious tree(s) were performed using tree bisection-reconnection (TBR) branch-swapping. 1000 random sequence addition replicates were used to minimize the chance of finding only locally optimal trees (Maddison, 1991). All sites were equally weighted and gaps treated as missing characters. We used nonparametric bootstrapping (Felsenstein, 1985) to measure support of clades with 1000 total pseudoreplicates and TBR branch-swapping with 2 random sequence addition replicates per pseudoreplicate.

For the maximum likelihood analysis the TrNef substitution model (rmat = 1.6386, 4.8769, 1.5625, 0.7506, 6.7754) with invariable sites (pinvar = 0.4065) and among-site rate heterogeneity ($\alpha = 0.8550$) was selected using hierarchical likelihood ratio tests implemented in Modeltest 3.06 (Posoda and Crandall, 1998). An heuristic search with 10 random sequence additions was used to find the optimal tree. We also performed likelihood bootstrapping with 300 total pseudoreplicates and TBR branch-swapping with 2 random sequence addition replicates per pseudoreplicate.

2.5.3. Bayesian analyses

To calculate posterior probabilities of clades, we used MrBayes 1.1 (Huelsenbeck, 2000) to run a 1,000,000 generation Markov chain under a GTR + G + I model sampling every 200 generations. We used the default (flat) priors for rate matrix (uniform 0–100), branch length (uniform 0–10), and tree topology parameters and ran one cold and three heated chains simultaneously. Visual inspection of samples from each scenario suggested that the Markov chain reached stationarity within 5000 generations but we discarded the first 30,000 generations to ensure that stationarity was reached. A majority rule consensus tree calculated from the 3500 remaining trees was constructed and used to determine the posterior probabilities of clades (Larget and Simon, 1999). To help ensure that the Markov chain was sampling from the posterior distribution, we repeated this analysis four times starting with random trees and examined the variance in posteriors attached to clades.

2.5.4. Hypothesis testing

We compared Gomon and Paxton's morphological topology to our molecular topologies in three ways. First, we conducted heuristic parsimony and likelihood searches using the morphological topology as a constraint (Fig. 1) and compared the raw scores of the constrained and unconstrained trees. Second, we performed the SH test (Shimodaira and Hasegawa, 1999) as implemented in PAUP*, comparing the best topology to the constrained topology using the RELL method for

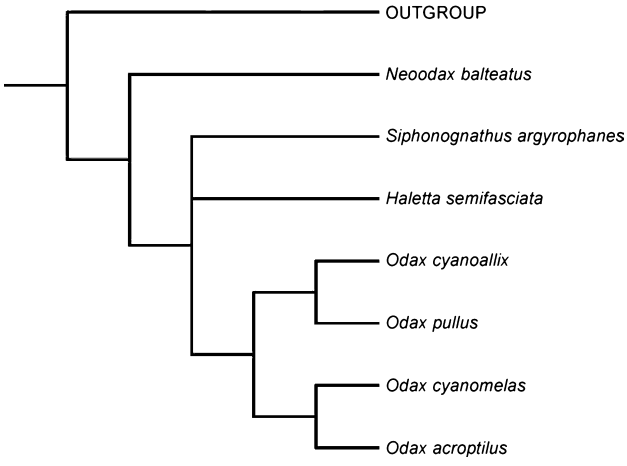

Fig. 1. Morphological hypothesis of odacine relationships. Shown is the odacine phylogeny proposed by Gomon and Paxton (1985) from their morphological study.

bootstrap replications (Goldman et al., 2000; Kishino et al., 1990; Shimodaira and Hasegawa, 1999). Finally, we calculated the posterior probability of the morphological hypothesis by counting the number of times that topologies congruent with the morphological constraint appeared in the MCMC sample from our Bayesian analysis.

Character states (i.e., herbivory, carnivory) were optimized on to the tree using maximum parsimony (Cunningham et al., 1998).

3. Results

3.1. Partition congruence

Two partition pairs showed significant incongruence with one another (16S vs. RAG2 and Tmo4C4 vs. RAG2) and a third approached significance (12S vs. RAG2; Table 3). Despite the apparent conflict in phylogenetic signal between RAG2 and the other partitions, the most parsimonious trees from individual gene analysis were largely congruent with one another and with the results of the combined analysis. Furthermore, all of the topological conflicts among gene partitions occurred at weakly supported nodes (BP $\leqslant$ 70%). Finally, within-odacine relationships were congruent with or identical to the relationships found in the combined data analysis. For these reasons, we interpreted the significance of the partition homogeneity test to be due to differences in size or levels of homoplasy within or among gene partitions (Dolphin et al., 2000; Dowton and Austin, 2002), rather than to strong conflict in signal, and we combined our data for subsequent analyses.

3.2. Tree construction

Maximum parsimony (MP) and maximum likelihood (ML) analyses produced nearly identical topologies (MP length = 2358, CI = 0.57, RI = 0.58; ML $-\ln L =$ 14174.55; Figs. 2 and 3), differing only in the placement of the clade *Cheilinus* + *Cryptotomus*. In ML analysis, this clade formed the sister group to a clade consisting of *Cheilio, Notolabrus, Halichoeres*, and *Coris.* In MP analysis, *Cheilinus* + *Cryptotomus* formed the sister group to *Lachnolaimus, Bodianus, Choerodon*, and the odacines. With the exception of the placement of *Cheilinus* + *Cryptotomus*, all clades in the MP analysis received high bootstrap support. Similarly, all clades in the ML analysis received high bootstrap proportions and high posterior probabilities. In addition, posterior probabilities calculated from repeated analyses using different starting trees were extremely similar to those shown in Fig. 2.

Choerodon anchorago formed the sister taxon to the odacines, rendering the three hypsigenyine taxa paraphyletic. Within the odacines, *O. cyanoallix* + *O. pullus* formed the sister group to the remaining ingroup members with *O. acroptilus, O. cyanomelas*, and *Siphonognathus argyrophanes* forming successively closer sister groups to the clade (*Haletta semifasciata* + *Neodax balteatus*). *Cheilio inermis* did not group with the odacines, but rather formed the sister taxon to a clade comprising the pseudolabrine *Notolabrus gymnogenis* and the julidines *Halichoeres hortulanus* and *Coris aygula*.

Table 3
Results of partition homogeneity test

	Partition			
	12S	16S	RAG2	Tmo4C4
12S	—	0.144	0.036	0.464
16S		—	**0.006**	0.287
RAG2			—	**0.002**
Tmo4C4				—

3.3. Hypothesis testing

The most optimal parsimony and likelihood trees found under the constraints of the Gomon and Paxton (1985) morphological topology were 76 steps and 164.33 log likelihood units, respectively, worse than the unconstrained topologies (Fig. 4). The SH test revealed that the unconstrained topology explained the data significantly better than the constrained tree ($P < 0.001$). Finally, the posterior probability of the constrained topology was very low: 100% of the marginal density on topology calculated from the MCMC samples was distributed over six topologies, each of which showed odacine relationships that were identical to those found in the unconstrained ML tree (Fig. 5).

4. Discussion

Our phylogenetic results support the hypothesis that the Labridae sensu Kaufman and Liem (1982) is monophyletic. The molecular phylogeny of the odacines shows that the group is a monophyletic clade within the basal hypsigenyine labrids, and we use the topology of the tree to draw conclusions regarding the close relatives of the odacines and odacine taxonomy within the Labridae. The topology of the tree differs from previous hypotheses and suggests that early odacine evolution was dominated by biogeography rather than habitat specialization, with a basal split between Australian and New Zealand clades. Lastly, the optimization of herbivory on the tree reveals the independent evolution of this character and associated morphological traits in the group, providing a case study for the acquisition of novel functional morphology among labrid fishes.

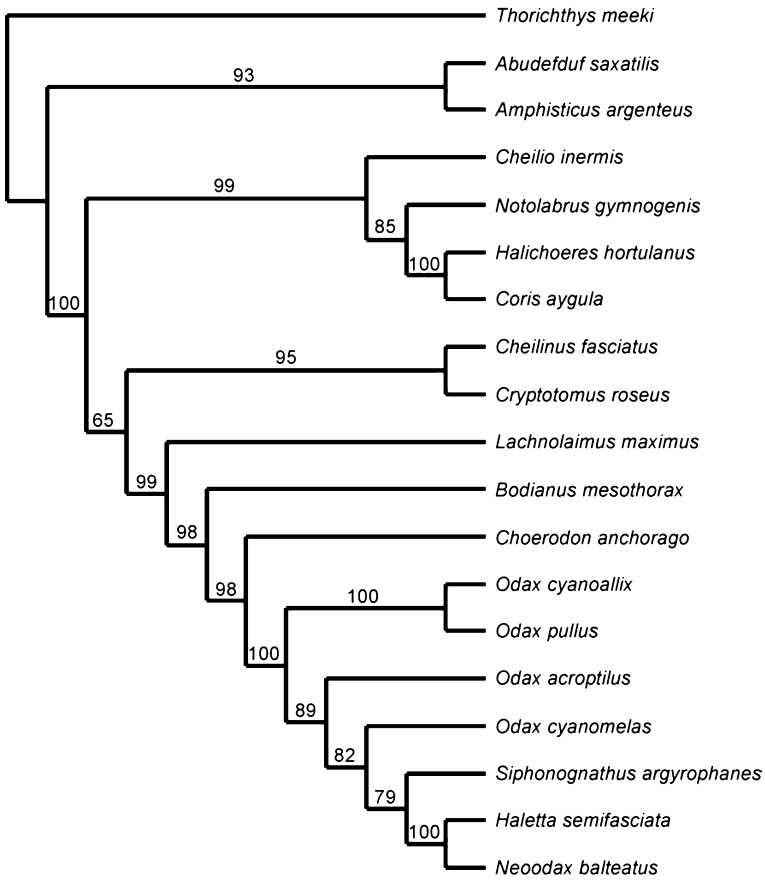

Fig. 2. Maximum parsimony phylogeny of the odacines. Shown is the single most parsimonious tree (length = 2358, CI = 0.57, RI = 0.58) resulting from heuristic searching (see Section 2). Numbers above branches are maximum parsimony bootstrap proportions calculated from 1000 pseudoreplicates.

4.1. Phylogeny and classification of odacines

The pattern of odacine relationships in our molecular phylogenetic analyses differs in three important respects from those described in previous studies. First, the placement of successive sister groups to the odacines (*Choerodon anchorago, Bodianus mesothorax, Lachnolaimus maximus*) received a high degree of statistical support, indicating that odacines are members of the labrid tribe Hypsigenyini. A sister group relationship between odacines and *Choerodon* is consistent with the biogeography of these taxa, since the latter genus is confined to the Indo-West Pacific, with nearly half of the species restricted to the Australian plate (Gomon, 1997). Corroborating our molecular placement of odacines with a morphological diagnosis of the hypsigenyines is problematical at this time since the single synapomorphy that Gomon (1997) identified for this group is a dental ridge on the inside of the prominent anterior canines of each jaw. Odacines have fused teeth, and so presumably have lost this character.

Together with the placement of scarines in our analyses, the placement of the odacines within the Hypsigenyini reinforces previous suggestions (e.g. Bellwood, 1990, 1994; Russell, 1988) that the Labridae *sensu* Greenwood et al. (1966) and Norman (1966) is paraphyletic. The scarines formed the sister group to the cheilines in all our analyses, although the placement of cheilines + scarines was criterion-dependent (i.e., sister group to the clade hypsigenyines + odacines under MP, and to *Cheilio* + julidines under ML). The phylogenetic relationships of labrid tribes will be developed in more detail elsewhere (Westneat et al., in prep.).

Second, *Cheilio inermis* appears to be a member of the pseudolabrine/julidine lineage, *contra* Gomon (1997) who placed it in the Odacini. The placement of *Cheilio* as sister to the clade pseudolabrines + julidines in our analyses is consistent with Günther (1861), Jordan and Snyder (1902), and Regan (1913). Günther (1861) erected six labroid subgroups, including Labrina, Hypsigenina, Julidina, Pseudodacina, Scarina, and Odacina. All known odacines were placed in the Odacina, and *Cheilio* was placed in the Julidina in a sub-group that included *Anampses, Hemigymnus, Stethojulis, Halichoeres, Thalassoma, Gomphosus, Coris, Novaculichthys*, and *Cymolutes*. Jordan and Snyder (1902) classified

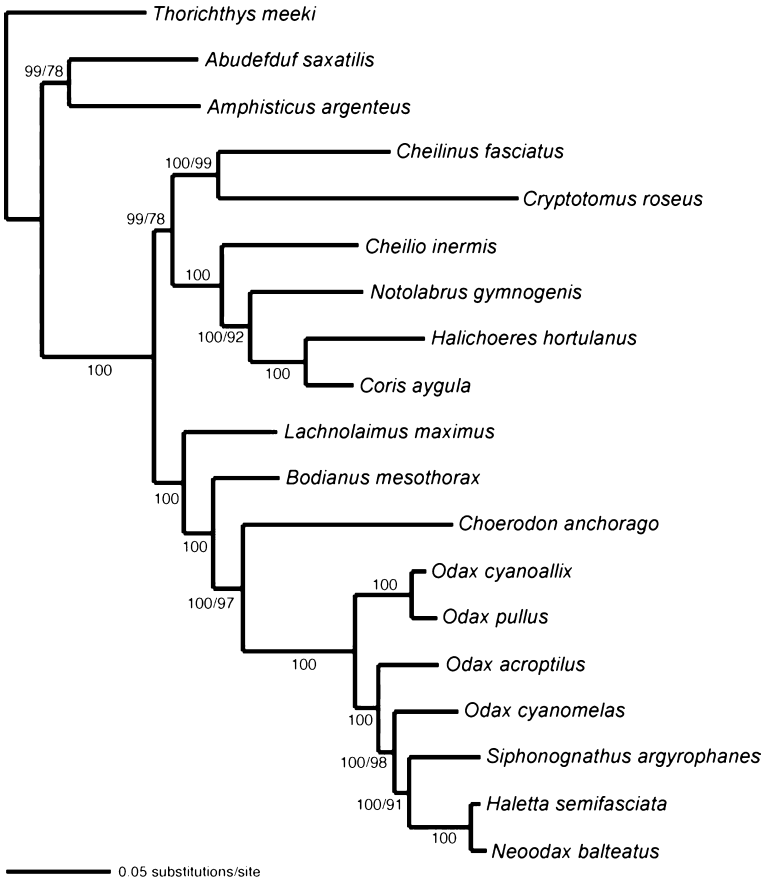

Fig. 3. Maximum likelihood phylogeny of the odacines. Shown is the single most likely phylogeny ($-\ln L = 14174.55$) resulting from heuristic searching under a TrNef + G + I model (see Section 2). Numbers on branches are posterior probabilities calculated from a one million generation MCMC chain followed by maximum likelihood bootstrap proportions calculated from 200 pseudoreplicates. A single number above a branch indicates that the posterior probability and the bootstrap proportion were the same.

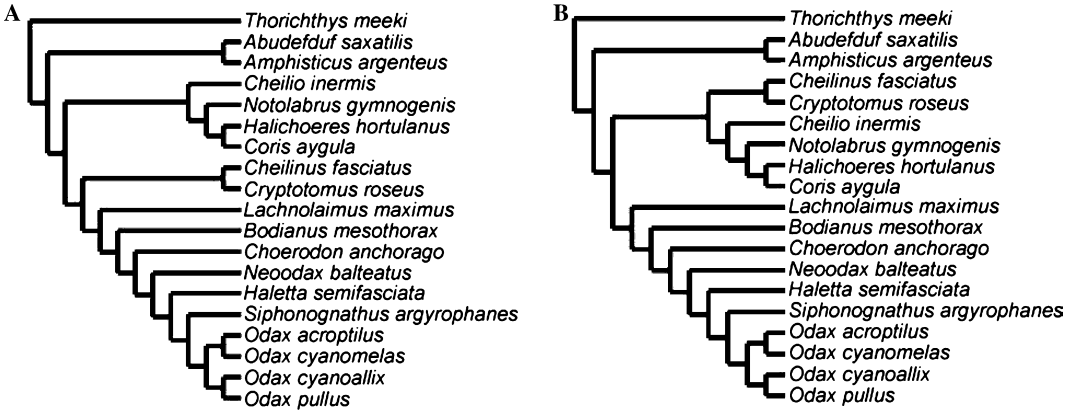

Fig. 4. Morphological constraint trees. (A) Maximum parsimony tree constrained to be congruent with the odacine morphological phylogeny of Gomon and Paxton (Fig. 1) (Gomon and Paxton, 1985). The constrained tree (length = 2434 steps) was 76 steps longer than the unconstrained tree (Fig. 2). (B) Maximum likelihood topology congruent with the morphological constraint tree. The constrained tree ($-\ln L = 14338.88$) was ~164 log likelihood units worse than the unconstrained tree (Fig. 3).

Cheilio in a subfamily Thalassominae with *Pteragogus, Anampses, Hemigymnus, Stethojulis, Halichoeres, Thalassoma, Gomphosus*, and *Coris*. Regan (1913) created the subfamily Julidinae to include 18 genera including *Cheilio* and many of the same genera that are now included in the Julidini of Gomon (1997).

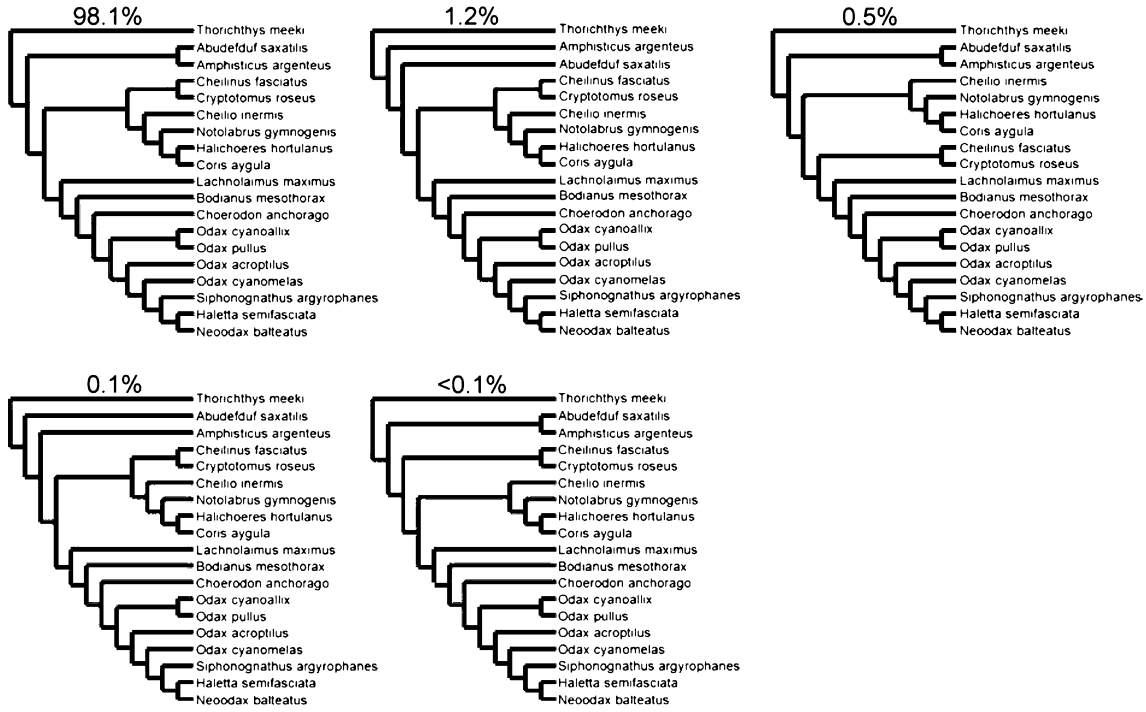

Fig. 5. Posterior probabilities of trees. The Markov-chain visited five unique topologies over a million generations with nearly all of the posterior density centered on the MAP tree. The position of *Lachnolaimus maximus, Bodianus mesothorax*, and *Choerodon anchorago* as successively closer sister groups to the odacines as well as relationships within the odacines themselves were identical across all sampled topologies. The 95% credible set contained a single tree with topology identical to that shown in Fig. 3. The 99% credible interval contained two trees that differed only in the arrangement of the non-labrid outgroups.

Third, the genus *Odax* was paraphyletic and basal to other odacine genera in all our analyses. Our MP and ML topologies explained the sequence data set significantly better than the previous morphological tree of Gomon and Paxton (1985), which placed *Neoodax* basal to an unresolved trichotomy between *Haletta, Siphonognathus*, and a monophyletic *Odax*. Most of the characters used by Gomon and Paxton (1985) to support a monophyletic *Odax* were associated with the oral and pharyngeal jaws (e.g., profile of premaxilla, location of symphyseal joint on dentary, shape of hyomandibula, dental surface of pharyngeal). It is thus possible that these characters are functionally related and represent either homoplasy or plesiomorphy (the evolution of jaw function in odacines will be discussed in a separate paper). Interestingly, the four *Odax* species were originally split across the three separate genera *Odax* Cuvier, 1829, *Olisthops* Richardson, 1850, and *Heteroscarus* Castelnau, 1872 (Gomon and Paxton, 1985; Scott, 1976) in a manner consistent with the monophyletic species groupings in our analysis. The phylogenetic relationships of *Odax* species in our analyses are consistent with a basal split between New Zealand (*O. pullus* and *O. cyanoallix*) and Australian (*O. acroptilus*, *O. cyanomelas*, *Siphonognathus*, *Haletta*, and *Neoodax*) clades. This finding has two important consequences for our understanding of odacine evolution: (i) species groups on either side of the Tasman Sea diverged early in odacine evolution, and (ii) either herbivory evolved twice in the odacines, or herbivory evolved once with two reversions to carnivory. We will discuss both of these points in more detail below.

4.2. Odacine biogeography

Basal divergences in the odacines relate to biogeography and not habitat. This pattern of divergence differs from that reported for scarines by Streelman et al. (2002), who infer an initial split into coral reef and seagrass clades. In odacines, evolutionary shifts between rocky reef and seagrass habitats are much harder to interpret, partly because of the heterogeneity of these habitat types in temperate Australia (Kendrick, 1999). *Odax cyanoallix* and *O. pullus* are found on algal dominated rocky reefs (Choat and Ayling, 1987), while *O. cyanomelas* and *O. acroptilus* predominantly but not exclusively occur in this habitat (Jenkins and Wheatley, 1998; Harman et al., 2003; Kuiter, 1993; MacArthur and Hyndes, 2001). *Haletta semifasciata* are largely restricted to seagrass areas, while *Neoodax balteatus*, *Siphonognathus* spp., and juvenile *Odax acroptilus* use both habitats (Gomon and Paxton, 1985; Jenkins and Wheatley, 1998; Kuiter, 1993; MacArthur and Hyndes, 2001; Scott, 1976). Determining the evolutionary polarity of habitat in odacines is further complicated since

Choerodon, the sister group to the odacines in our analysis, includes species that range from strongly reef-associated to those that frequently occur in seagrass areas (Randall et al., 1997).

The lack of a fossil record for odacines, and the poor early fossil record for labrids in general, greatly hamper our ability to reconstruct the evolutionary history of odacines. The hypsigenyine labrids, which include the sister group to the odacines, can be characterized on the basis of their phyllodont pharyngeal dentition and are known from Eocene deposits in Italy and Antarctica (Bellwood, 1990; Bellwood and Wainwright, 2002). *Phyllopharyngodon longipinnis* was described from the early-middle Eocene (50 mya) Monte Bolca deposit by Bellwood (1990), while Long (1992) described a slightly younger (47.4–44.5 mya; Dutton et al., 2002) Mid-Eocene form from the La Meseta Formation of Seymour Island. The Monte Bolca deposit represents a shallow-water tropical assemblage from near the center of the Tethyan Sea (Bellwood, 1996), although the precise nature of the habitat is equivocal (Bellwood, 1998; Robertson, 1998). The La Meseta Formation stratum in which the hypsigenyine fossil was found represents a shallow-water cool to warm temperate assemblage (Dutton et al., 2002; Stilwell and Zinsmeister, 2000), at a time when Australia and New Zealand were much closer to Antarctica and before the formation of the East Antarctic ice sheet and the development of the modern Southern Ocean circulation (Cooke et al., 2002; Crame and Rosen, 2002; Nelson and Cooke, 2001).

The current range of odacines is largely restricted to temperate waters, although *Odax cyanomelas* reaches the subtropical Houtman Abrolhos Islands in Western Australia and northern New South Wales on the east coast of Australia (Gomon and Paxton, 1985). The present distribution of odacines thus suggests that their recent history is associated with temperate waters (Gomon and Paxton, 1985), but has this always been the case? An answer to this question rests partly on the timing of odacine divergence from other hypsigenyines. A transversion rate of 0.14% per million years for the 12S and 16S genes (Bernardi et al., 2000; Streelman et al., 2002) yields a mean divergence date of about 38 mya between the odacine species and *Choerodon anchorago*. Although this estimate should be treated with great caution, it is consistent with the hypsigenyine fossil record.

A late Middle Eocene odacine divergence corresponds to a period when sea temperatures around New Zealand and southern Australia were temperate to subtropical (Buening et al., 1998; Nelson and Cooke, 2001). The region cooled near the Eocene/Oligocene boundary (Buening et al., 1998), warmed again in the early middle Miocene (Feary and James, 1998; Gallagher et al., 2001), and then underwent a period of prolonged cooling from the Late Miocene (Gallagher et al., 2001). In general since the Eocene the oceanographic environment in most parts of southern Australia and New Zealand has fluctuated between cool temperate and subtropical as the development of the Southern Ocean circulation counterbalanced the tectonic drift of the region into lower latitudes (Feary and James, 1998). Present distribution suggests a mainly temperate water history for the odacines, and this is also supported by physiological evidence; *Odax pullus* appears to be near its temperature limit in summer in northern New Zealand (Brix et al., 1998). The hypsigenyine ancestors of odacines probably formed part of the temperate Wedellian marine assemblages that inhabited the Pacific margins of southern South America, West Antarctica, New Zealand, and south-eastern Australia until at least the late Eocene (Crame, 1999; Stilwell and Zinsmeister, 2000), when the distribution of these assemblages contracted as the cooling of the Southern Ocean intensified (Crame and Rosen, 2002; Lawver and Gahagan, 1998; Nelson and Cooke, 2001; Williams et al., 2003).

4.3. The evolution of herbivory in odacines

The hypsigenyine sister taxa of odacines are all carnivores, raising the question of when herbivory evolved in the odacines. *Odax cyanoallix*, *O. cyanomelas*, and *O. pullus* are unusual among marine herbivorous fishes in that they live in temperate waters, show few anatomical specializations for herbivory, feed on fucoid and laminarian macroalgae, and have high levels of microbial fermentation in the hindgut (Ayling and Paxton, 1983; Clements et al., 1994; Mountfort et al., 2002). There does not appear to be any real structural modification of the alimentary tract in herbivorous odacines (Clements and Bellwood, 1988), although there may be physiological differences (Clements and Rees, 1998). The most obvious differences between carnivorous hypsigenyines and herbivorous odacines are (i) fusion of the teeth in the oral jaws to produce a single, cutting edge, and (ii) confinement of the dentigerous surface on the upper and lower pharyngeal bones into raised ridges (Clements and Bellwood, 1988; Gomon and Paxton, 1985). Both of these changes are consistent with efficient harvesting and processing of tough, phaeophyte thallae (Clements and Bellwood, 1988).

Optimising the evolution of herbivory on our odacine phylogeny suggests that herbivory arose twice independently in the lineages leading to *O. pullus*/*cyanoallix* and to *O. cyanomelas*. The alternative, that herbivory evolved once, is less parsimonious as it requires three character changes: gain of herbivory in the common odacine ancestor, and then separate reversions to carnivory both in *O. acroptilus* and the ancestor of the clade containing *Siphonognathus*, *Haletta*, and *Neoodax*. The less parsimonious hypothesis, that herbivory arose once in the odacines, is more consistent with odacine biology

for two reasons. First, the herbivory-twice hypothesis fails to explain the origin of the fused beak in the common ancestor of all odacines. Herbivorous odacines have tight linkages between premaxilla and maxilla that limit jaw protrusion (Clements and Bellwood, 1988), and lack the additional jaw linkages that are associated with scraping and excavating in scarines (Bellwood and Choat, 1990). Carnivorous odacines feed mainly on crustaceans (Gomon and Paxton, 1985; Scott, 1976), except for *O. acroptilus* that also eat detritus, gastropods, and bryozoans (Choat and Clements, 1992). No extant odacines are durophagous, and none selectively ingest sessile invertebrates (e.g., bryozoans) associated with phaeophyte thallae. Overall, it is hard to explain odacine jaw structure in terms of scraping, durophagy or the capture of evasive prey. Second, since all herbivorous odacines have a carnivorous post-settlement phase (Clements and Choat, 1993), evolutionary reversion to carnivory in herbivorous odacines can be readily explained through neoteny. *Siphonognathus* spp., *N. balteatus*, and *H. semifasciata* resemble the juveniles of herbivorous odacines both in terms of body shape and diet. Whether ancestral odacines were carnivorous or herbivorous, the dietary variation apparent in extant species casts doubt on the suggestion that the evolution of jaw structures employed in herbivory constrain feeding repertoires in fish evolution (Streelman and Danley, 2003). Additional experimental work on odacine feeding biomechanics and morphological analysis of cranial levers and linkages (Westneat, 1995) may clarify this issue.

In conclusion, this study demonstrates that odacines are deeply nested within the labrid tribe Hypsigenyini. The purported odacine *Cheilio inermis* is distinct, forming part of the julidine lineage. These results highlight two features of morphological evolution within the Labridae: (i) that novel feeding modes have evolved repeatedly in the group, and (ii) that there is considerable convergence in external morphology due to independent radiation of sub-clades. Whether herbivory evolved once (ancestrally) or twice (convergently) in the odacines is uncertain. A reconsideration of characters associated with herbivory in light of the phylogeny suggests that herbivory evolved once in ancestral odacines, with two subsequent reversions to carnivory. We will explore the evolution of herbivory further in future work by examining odacine jaw mechanisms in more detail. Of particular interest is the extent to which the characteristic fused beak of odacines constrains capture of mobile, animal prey. Although limited in species diversity and distribution, the odacines are of interest because of their extraordinary morphological disparity and their evolution of novel feeding mechanisms. The unexpected phylogenetic results of this study suggest that more surprises are in store for biologists studying evolution in labroid fishes.

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