

Research article

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Macroevolutionary analysis of the tempo of diversification in snappers and fusiliers (Percomorpha: Lutjanidae)

Bruno Frédéricich^{1,2,*} & Francesco Santini³

¹Laboratoire de Morphologie Fonctionnelle et Evolutive, AFFISH Research Center, Université de Liège, 4000 Liège, Belgique.

²Laboratoire d'Océanologie, MARE Center, Université de Liège, 4000 Liège, Belgique.

³Associazione Italiana per lo Studio della Biodiversità, 56100 Pisa, Italy.

* Corresponding author: bruno.frederich@ulg.ac.be

Email: francesco.santini@alumni.utoronto.ca

ABSTRACT. The percomorph fish family Lutjanidae (snappers and fusiliers) includes about 135 reef-dwelling species, mainly confined to tropical and subtropical marine waters. The great majority of snappers are active predators feeding on fishes or crustaceans, even though some species, including the fusiliers (Caesioninae), have evolved zooplanktivory. Lutjanids show a great diversity of habitat preferences, based on depth segregation and distribution across reef and associated habitats (e.g., mangroves, seagrass beds, estuaries). In spite of their great ecological and economic importance little is known about the tempo of evolution in this group. The present study provides the most comprehensive molecular phylogeny to date for lutjanids, including 70% of extant species and 19 of the 21 currently described genera. We time-calibrated our molecular tree using the oldest described lutjanid fossils, and show how this group most likely originated during the Late Cretaceous or Early Paleocene. Lutjanids experienced a significant radiation during the Late Eocene and Early Oligocene, in contrast to a pattern of Late Oligocene/Miocene radiation observed in many other reef-associated groups. The time-tree allows us to investigate the tempo of diversification, and our results suggest a variation in the rate of speciation during the evolution of the major clade formed by “lutjanins and caesionins”. Variation in diet and life history strategies could explain this clade-specific dynamic, although future phylogenetic comparative studies combining additional ecological and morphological data are needed to test this hypothesis.

KEY WORDS. *Lutjanus*, phylogeny, ecological radiation, lineage diversification, molecular clock.

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Introduction

Snappers and fusiliers (Lutjanidae) include about 135 extant species of medium-sized to large fishes (FROESE & PAULY 2016; ESCHMEYER *et al.* 2016). Lutjanidae represents a successful radiation of reef- and mangrove-associated percomorphs in marine and brackish coastal waters across the tropical and subtropical oceans. Many species of snappers are the target of commercial fisheries in tropical areas, and they are considered one of the most important components of artisanal fisheries across many tropical countries (ALLEN 1985).

TABLE 1

Taxonomic diversity of Lutjanidae. The total number of species (data obtained from IWATSUKI *et al.* 2015; FROESE & PAULY 2016; ESCHMEYER *et al.* 2016) and the number of species included in our time-calibrated phylogeny (N) are provided. Numbers in brackets refer to the total number of species included in each subfamily.

Taxon	Genus	N _{TOTAL}	N
Apsilinae (12)	<i>Apsilus</i>	2	1
	<i>Lipocheilus</i>	1	-
	<i>Paracaesio</i>	8	2
	<i>Parapristipomoides</i>	1	-
Etelinae (20)	<i>Aphareus</i>	2	2
	<i>Aprion</i>	1	1
	<i>Etelis</i>	5	4
	<i>Pristipomoides</i>	11	7
	<i>Randallichthys</i>	1	1
Paradicichthyinae (2)	<i>Symphorus</i>	1	1
	<i>Symphorichthys</i>	1	1
Lutjaninae (78)	<i>Hoplopagrus</i>	1	1
	<i>Lutjanus</i>	71	54
	<i>Macolor</i>	2	2
	<i>Ocyurus</i>	1	1
	<i>Pinjalo</i>	2	2
	<i>Rhomboplites</i>	1	1
Caesioninae (23)	<i>Caesio</i>	9	4
	<i>Dipterygonotus</i>	1	1
	<i>Gymnocaesio</i>	1	1
	<i>Pterocaesio</i>	12	7
TOTAL		135	94

The family Lutjanidae is composed of 21 genera distributed into five subfamilies: Apsilinae, Etelinae, Paradicichthyinae, Lutjaninae and Caesioninae (Table 1 - JOHNSON 1993; MILLER & CRIBB 2007). With 71 known species, the genus *Lutjanus* includes most of the taxonomic diversity of the family (IWATSUKI *et al.* 2015; FROESE & PAULY 2016). Snappers are active predators, with most species feeding on fishes or large crustaceans using their powerful caniniform teeth (ALLEN 1985). Both the fusiliers, a lineage of open-water dwellers, as well as several additional snappers with a relatively slender, fusiform body shape and a forked caudal fin (e.g., *Ocyurus*, *Paracaesio*, *Pristipomoides*, *Rhomboplites*) have, however, evolved a zooplanktivorous diet (ALLEN 1985).

There is a strong variation of habitat preferences among lutjanids. Indeed, most species live in shallow waters less than 100 m deep (e.g., *Aprion*, *Lutjanus*, *Symphorichthys* and *Symphorus*), while others, such as *Paracaesio*, are found at intermediate depth (100–200 m), and the species of the genera *Etelis* and *Aphareus* live in waters up to 500 m below the surface (NEWMAN & WILLIAMS 1996). Numerous species of *Lutjanus* experience ontogenetic habitat shifts, and some are mangrove- or estuarine-dependent for the completion of their juvenile phase (e.g., NAGELKERKEN *et al.* 2000; ABURTO-OROPEZA *et al.* 2009). During growth these species of *Lutjanus* show an ontogenetic shift from mangroves and estuaries to deeper, offshore coral reef environments. However some species, such as *Lutjanus griseus* (Linnaeus, 1758), may also occur in estuarine mangroves when adults (NAGELKERKEN *et al.* 2000).

In spite of the ecological and economic importance of this group, we currently do not have a densely-sampled phylogeny for this clade. All studies published to date include only a handful of lutjanid species, often from geographically restricted regions or from restricted clades (SARVER *et al.* 1996; ZHOU *et al.* 2004; ZHU *et al.* 2006; GOLD *et al.* 2015; WAKEFIELD *et al.* 2016; ANDREWS *et al.* 2016). For example, MILLER & CRIBB (2007) investigated the relationships among 27 species of Indo-Western Pacific (IWP) snappers while the studies of GOLD *et al.* (2011) included 20 species, 13 of which originated from the Western Atlantic or Eastern Pacific. The most extensive molecular phylogeny of snappers published to date only includes 43 species, representing around 32% of the extant diversity of the family (CHU *et al.* 2013). Moreover, none of these studies took advantage of the fossil record of lutjanids to produce a timescale of snapper evolution. Only GOLD *et al.* (2011) used a strict clock approach and a fixed rate of molecular evolution inferred from studies of previous groups to produce a time-tree for the lutjanid subclade of their study. In addition to the absence of a large-scale phylogenetic hypothesis of lutjanid intra-relationships, we are also lacking a macroevolutionary study looking at the tempo of evolutionary diversification of this group.

In the present study, we used a supermatrix approach to assemble a dataset containing four loci for 94 species of lutjanids (i.e., 70% of the extant diversity). Our molecular phylogeny was then time-calibrated using the oldest described lutjanid fossils and used as a framework to explore the tempo of lineage diversification.

Materials and Methods

Data acquisition and sampling

Our molecular data set includes 94 species of Lutjanidae representing 19 of the 21 currently described genera (Tables 1, S1), with only the two monotypic genera *Lipocheilus* and *Parapristipomoides* missing. We used the PhyLoTa browser version 1.5 (SANDERSON *et al.* 2008) to obtain sequences for four loci that had the highest number of sequences available for lutjanids: the nuclear *Rag1* and the mitochondrial *cox1*, *Cytb*, and *16s* (Table S1). As the current version of PhyLoTa is based on release 194 of GenBank (from February 15, 2013), we added more recent sequences for the species in our sampling directly from GenBank.

It is not currently known with certainty which percomorph lineage is the sister group of the lutjanids. Most recent studies investigating teleost fish deep level relationships suggest the existence of a group formed by Lutjanidae, Haemulidae (grunts) and Malacanthidae (tilefishes) (BETANCUR-R *et al.* 2013; NEAR *et al.* 2013; RABOSKY *et al.* 2013). We thus selected as outgroups two species of Haemulidae, the group that most frequently appears as the sister taxon to lutjanids (BETANCUR-R *et al.* 2013; NEAR *et al.* 2013; RABOSKY *et al.* 2013).

Phylogenetic analyses

We used the MUSCLE aligner (EDGAR 2004) available in MEGA 6 (TAMURA *et al.* 2013) to align the individual gene datasets using the default setting, and then visually inspected the alignments to ensure that these would be biologically accurate. We trimmed the 3' and 5' ends of the alignments in order to minimize the amount of missing data, and concatenated the four loci using Mesquite 3.01 (MADDISON & MADDISON 2015). Our final data matrix consisted of 1371 base pairs (bp) for *Rag1*, 600 bp for *16s*, 651 bp for *cox1*, and 954 bp for *Cytb*, for a total of 3576 nucleotides. We used PartitionFinder v1.1.1 (LANFEAR *et al.* 2012) to identify the optimal set of partitions of the data and select the best fitting models of sequence evolution for each of these from the pool of models implemented in BEAST 1.8 (DRUMMOND & RAMBAUT 2007) using Bayes factor scores (BIC). We did not include models that have both the gamma parameter and the proportion of invariant sites parameter, as this last parameter is already accounted for by the gamma (YANG 2006). The partitions and selected models are listed in Table 2.

TABLE 2

Models of sequence evolution selected by PartitionFinder under the corrected Akaike Information Criterion scores (AICc).

Best model	Subset partitions	Subset sites
TrN+G	cox1_1, cytb_1	1-651\3, 652-1605\3
HKY+I	cox1_2, cytb_2	2-651\3, 653-1605\3
TrN+G	cox1_3	3-651\3
GTR+G	cytb_3	654-1605\3
SYM+G	16s	1606-2205
HKY+I	rag1_1, rag1_2	2206-3576\3, 2207-3576\3
HKY+G	rag1_3	2208-3576\3

We performed Bayesian analyses using MrBayes 3.2 (RONQUIST *et al.* 2012) after each partition had been assigned the model selected by PartitionFinder (LANFEAR *et al.* 2012). The models not implemented by MrBayes, such as variations of the TrN, were replaced by the closest model (GTR). We ran two analyses for 25 million generations each with four chains (three heated, one cold) and sampling every 1000 generations. We visually inspected the trace files in Tracer 1.6 (DRUMMOND & RAMBAUT 2007) to verify that the chains had reached convergence. After discarding the first 12.5 million generations as burnin, we combined the remaining trees to obtain a 50% majority rule consensus tree.

In order to use the molecular dataset to infer a time-calibrated phylogeny, we used the uncorrelated lognormal priors enforced in BEAST 1.8 (DRUMMOND & RAMBAUT 2007). The oldest known lutjanid fossil that has been referred to the crown snappers is *Hypsocephalus atlanticus* Swift & Ellwood, 1972 from the *Operculinoides ocalanus-Asterocyclina* Zone of the Crystall River Formation, Ocala group, which has been referred to the uppermost Late Eocene of Florida (SWIFT & ELLWOOD 1972). These sediments date to the very end of the Eocene and the beginning of the Oligocene. We thus use the Eocene–Oligocene boundary to set a minimum age of 33.9 Ma for this fossil, which is thought to be a close relative of the extant *Hoplopagrus guntheri* Gill, 1862. As *Hoplopagrus* is recovered within the clade “*Lutjanus*”, and the relationships among some of the most basal nodes within this clade are not strongly supported, we used this fossil calibration to set a minimum age on the clade “*Lutjanus*”. Currently there are six fossils from the Middle Eocene deposits of Bolca (Italy, dated at ~ 50 Ma; CARNEVALE *et al.* 2014) that have been identified as Lutjanidae (BANNIKOV 2006), even though their placement has not yet been supported by a comparative morphological phylogenetic study and some of these fossils may lack synapomorphies of extant lutjanids identified by JOHNSON (1980) (G. Carnevale, pers. comm.). For the purpose of our analysis we treat these fossils as stem lutjanids, providing an age of 50 Ma for the soft upper boundary on this calibration. We also assigned a prior to the root of our tree. As there are no fossils that can convincingly date the split between lutjanids and haemulids, we used a normal distribution with a mean age of 67 Ma and an SD of 10 Ma. This choice produces a 95% probability that lutjanids and haemulids separated between 50 Ma, age of the putative stem lutjanids from Bolca, and 83.5 Ma, age of the Calcarei di Melissano Formation from Nardò (Italy), which contains several records of fossil percomorphs (see supplementary material in CHEN *et al.* 2014 for justification of the age).

All partitions were assigned the same model selected by PartitionFinder (LANFEAR *et al.* 2012), and a birth-death prior with incomplete sampling was assigned to the rates of cladogenesis. We ran four sets of analyses with 50 million generations each, and sampling every 10000 generations. We used Tracer 1.6 (DRUMMOND & RAMBAUT 2007) to inspect the chains for convergence, which we interpreted to have

occurred when the ESS for all parameters was over 200. As the chains reached convergence very rapidly, we removed the first 10% of the trees as burnin, used LogCombiner to merge the remaining trees, and used TreeAnnotator (DRUMMOND & RAMBAUT 2007) to obtain a consensus time-tree.

Lineage diversification

We explored the tempo of lineage diversification by computing the gamma (γ) statistic, which indicates the extent to which a phylogeny differs from branching events expected under a constant-rate process. A negative γ value indicates that the internal nodes of the tree are closer to the root, supporting a model of early diversification. We then assessed the significance of γ statistic using the Monte Carlo constant rates (MCCR) test of PYBUS & HARVEY (2000), which accounts for incomplete taxon sampling. We also assessed the fit of four models of clade accumulation to the branching times in our phylogeny. We compared two constant rate models (Yule and birth-death) to two density-dependent speciation rate models, predicting slowdowns in the tempo of diversification [density-dependent exponential (DDX) and density-dependent logistic (DDL) following RABOSKY & LOVETTE 2008]. We used Akaike's Information Criterion (AIC) scores and weights to compare the fit of the models. A ΔAICc value of four or more was taken as an indication of support for one model over the others following BURNHAM & ANDERSON (2002). The MCCR test, the γ statistic and diversification model fitting were computed using the LASER package (Version 2.4.1; RABOSKY 2006) for R (R DEVELOPMENT CORE TEAM, 2015).

Results

Phylogenetic analyses and divergence time estimates

The topologies of the Bayesian analyses confirm the non-monophyly of lutjanids without the inclusion of the caesionins, a result already shown by previous molecular studies (MILLER & CRIBB 2007). A number of highly supported clades are identified, even though some of the deeper nodes of the tree have poor posterior probability (PP) support, and some polytomies appear toward the more recent part of the phylogeny (Fig. 1). Several of the traditional genera, including *Lutjanus* (the richest genus in terms of species number; Table 1), are non-monophyletic.

In our analysis, *Apsilus dentatus* Guichenot, 1853, *Paracaesio*, Valenciennes, 1830, *Etelis*, *Randallichthys*, *Aphareus* and *Pristipomoides* are grouped together and are found to be sister taxa of the remaining lutjanids (Fig. 1). Within this subclade including seven different genera, *Apsilus dentatus* and *Paracaesio* are sister taxa to a subclade that includes *Aprion virescens* + *Randallichthys* + *Etelis* as well as a paraphyletic *Pristipomoides*, which includes *Aphareus*. Within the other subclade, *Symphorichthys* and *Symphorus* form a well-supported monophyletic assemblage sister to all remaining lutjanids, i.e., the lutjanins and caesionins (here referred as "lutjanins + caesionins" clade). The next lineage to branch off includes *Lutjanus adetii* (Castelnau, 1873) and *Lutjanus sebae* (Cuvier, 1816), sister to *Pinjalo pinjalo* (Bleeker, 1850), several additional species of *Lutjanus* [*L. timoriensis* (Quoy & Gaimard, 1824), *L. sanguineus* (Cuvier, 1828), *L. erythropterus* Bloch, 1790 and *L. malabaricus* (Bloch & Schneider, 1801)] and *Pinjalo lewisi* Randall, Allen & Anderson, 1987 (clade A, Fig. 1). *Hoplopagrus guentherii* is then shown to be the sister taxon to a large clade, combining clade B and clade C (Fig. 1). *Lutjanus gibbus* (Forsskål, 1775), *Macolor* and the caesionins (*Caesio*, *Pterocaesio*, *Dipterygonotus balteatus* and *Gymnocaesio gymnoptera*, with both *Caesio* and *Pterocaesio* shown to be non-monophyletic) form clade B. The clade C (Fig. 1) includes several lineages that form the bulk of the diversity within *Lutjanus*, and among which the relationships are relatively unresolved. One of these subclades also includes the last two remaining genera within our sampling: *Ocyurus* and *Rhomboplites*.

The topologies produced by the Beast analyses closely match those of the MrBayes analyses, although they provide increased resolution towards the youngest nodes of the tree. In the analyses (Fig. 2), the stem age of the lutjanids is ~ 62 Ma while the age of crown lutjanids is ~ 54 Ma (45–66 Ma 95% Highest Posterior Density, HPD). The *Apsilus*, *Paracaesio*, *Aprion*, *Etelis*, *Randallichthys*, *Aphareus* and *Pristipomoides* clade is Middle Eocene in age (47 Ma, 37–58 Ma 95% HPD). Within this clade,

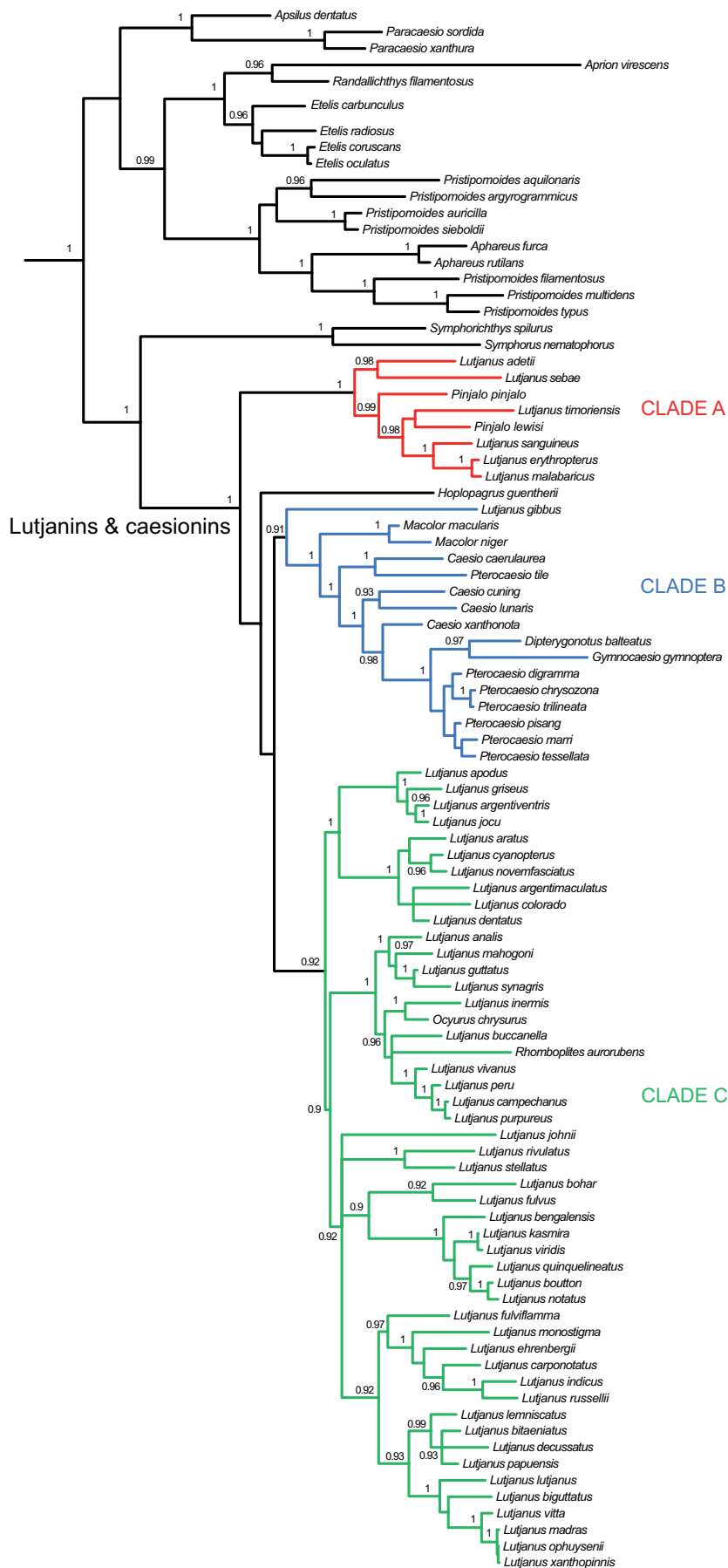


TABLE 3

Results from fitting models of lineage diversification. The models are ranked from best to worst, according to AIC scores and Akaike weights (wtAIC). Δ AIC scores indicate the difference between the candidate model and the best-fitting model. The initial speciation rate (r) and, if applicable, an additional model-specific parameter, are provided.

Clade	model	AIC	Δ AIC	wtAIC	r	Parameter
Entire time-tree	DDL	20.38	0.00	0.62	0.097	165.9
	DDX	22.68	2.30	0.20	0.134	0.194
	Pure birth (Yule)	23.44	3.06	0.13	0.066	–
	Birth-death	25.44	5.06	0.05	0.066	0.000
Clade “lutjanins & caesionins”	DDL	19.55	0.00	0.63	0.132	109.5
	DDX	21.08	1.53	0.30	0.253	0.333
	Pure birth (Yule)	24.58	5.03	0.05	0.079	–
	Birth-death	26.58	7.03	0.02	0.079	0.000

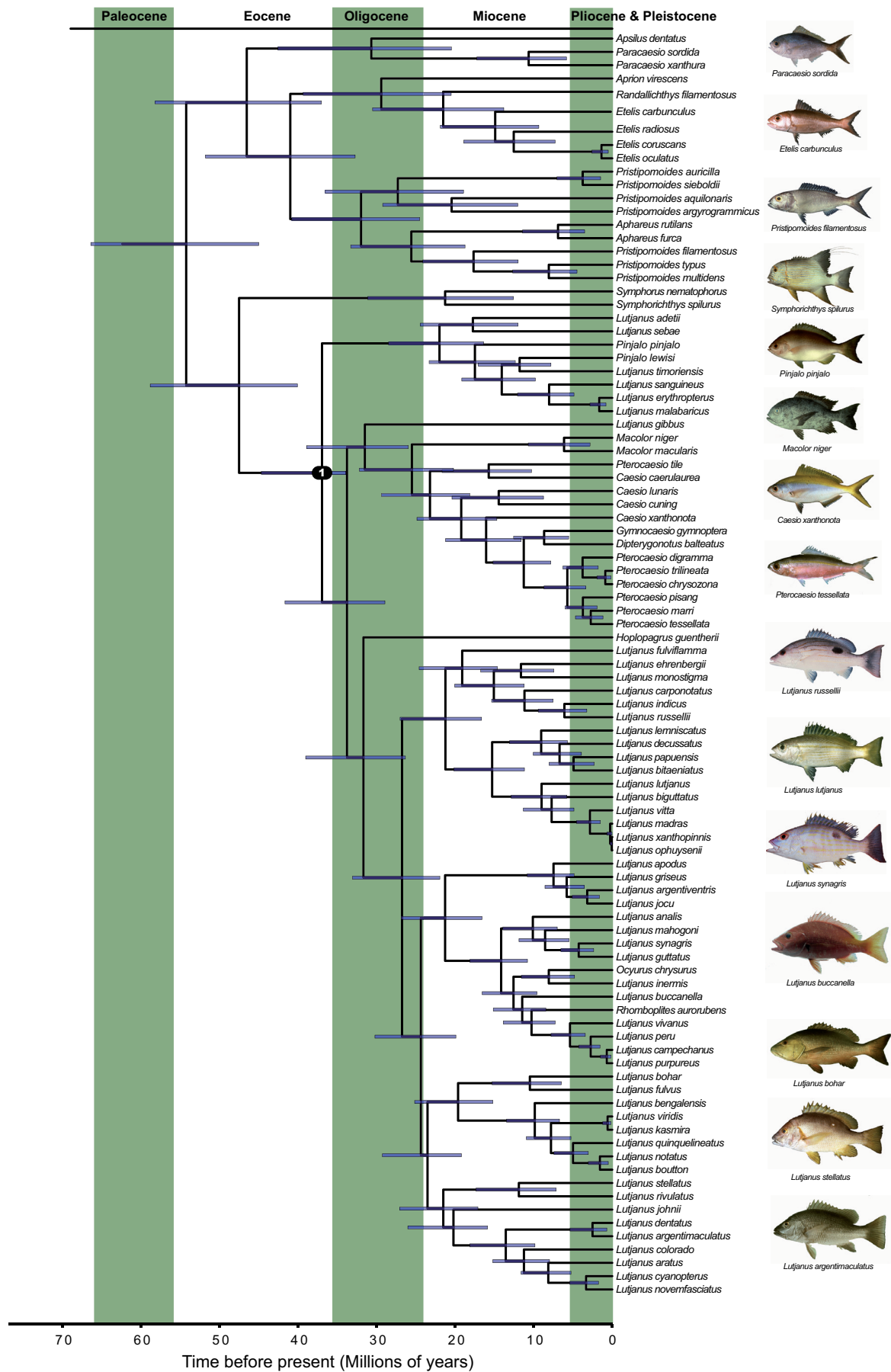
the paraphyletic *Pristipomoides* is 32 Ma (25–41 Ma 95% HPD), while *Etelis* is 15 Ma (9–21 Ma 95% HPD). The *Symphorichthys* + *Symphorus* clade dates to 21 Ma (13–31 Ma 95% HPD) and splits from the “lutjanins + caesionins” clade around 48 Ma (40–58 Ma 95% HPD). The crown age of the paraphyletic *Lutjanus* clade is ~ 37 Ma (30–45 Ma 95% HPD). The crown fusilier subclade originates in the Early Miocene, ~ 23 Ma (18–29 Ma 95% HPD), while the group that includes the majority of the species currently assigned to *Lutjanus* splits from *Hoplopagrus* around 32 Ma (26–39 Ma 95% HPD) and starts radiating towards the end of the Oligocene, ~ 27 Ma (21–33 Ma 95% HPD).

Lineage diversification

The MCCR test finds some evidence for a slowdown in the diversification rate during the evolution of Lutjanidae but this result is not significant ($\gamma = -2.72$, $P = 0.16$). The comparison of the fit of the diversification models fails to find strong support for constant rate models over diversity-dependent ones, and a pure birth model of diversification cannot be rejected (Table 3).

Lutjaninae and Caesioninae form a clade (Figs 1–2) including most of the taxonomic diversity of Lutjanidae ($N = 101$ species, i.e., 75% of the family). Thus, we have repeated the comparative analyses on this major clade. We find evidence for a slowdown in the diversification rate during the evolution of this clade ($\gamma = -2.35$, $P = 0.04$), a result confirmed by visual inspection of the lineage-through-time plot (Fig. 3). Accordingly, the two density-dependent models (DDL and DDX) are the best-supported models and together account for 93% of the Akaike weight (Table 3). This result from models fitting suggests that high rates of lineage diversification occurred during the early history of the “lutjanins & caesionins” clade, followed by a subsequent slowdown in diversification rate.

Figure 1 (opposite page) – Bayesian phylogenetic hypothesis inferred with MrBayes 3.2.6. Values above branches indicate posterior probabilities (PP) over 0.90. Clades A, B & C from the “lutjanins and caesionins” are illustrated in different colours.



Discussion

Phylogeny, fossil record and timescale of lutjanids

Our phylogenetic study based on the analysis of ~3.6 kb of mitochondrial and nuclear DNA sequences provides (1) the first densely-sampled molecular tree of snappers and allies, and (2) the first timescale for the entire group based on fossil lutjanid calibration points. Our analyses infer results that are congruent with the previous - and more limited - studies in showing that zooplanktivorous caesionins originated within the subfamily Lutjaninae, a group known to include species that mostly feed on fishes or benthic crustaceans (MILLER & CRIBB 2007). We also corroborate earlier findings that the most species-rich genus, *Lutjanus*, is not monophyletic (MILLER & CRIBB 2007; GOLD *et al.* 2011). Our phylogenetic study shows that several additional genera (e.g., *Pristipomoides*, *Pinjalo*, *Caesio*, *Pterocaesio*) are in need of revision due to their non-monophyly. Unfortunately the fossil record of the lutjanids remains relatively understudied, when compared to that of several other reef-associated groups that are abundant in the Bolca deposits (e.g., acanthurids, BLOT & TYLER 1990; TYLER 1999, 2005a, 2005b; TYLER & BANNIKOV 2000; pomacentrids, COOPER & SANTINI 2016; tetraodontiforms, TYLER & SANTINI 2002; SANTINI & TYLER 2003). The fish assemblage from Monte Bolca, Italy (Ypresian, ~ 50 Ma) includes at least six species that have been tentatively identified as lutjanids: *Ottaviana mariae* Sorbini, 1983 and *O. leptacanthus* (Agassiz, 1839), *Veranichthys ventralis* (Agassiz, 1839), *Goujetia crassispina* (Agassiz, 1839), *Lessinia horrenda* Bannikov & Zorzin, 2014 and *Lessinia* sp. (BANNIKOV 2006; CARNEVALE *et al.* 2014). The lack of a thorough morphological analysis of lutjanid synapomorphies (JOHNSON 1980) within these fossils currently prevents us from knowing with certainty whether they are all stem lineages or if some of them might fall within the crown snapper clade. This fact may have some important implications for the molecular dating. The oldest fossil that can currently be assigned with certainty to the crown lutjanids is the Late Eocene *Hypsocephalus atlanticus* from Florida, found in deposits that are about 16 Ma younger than Bolca (SWIFT & ELLWOOD 1972). The molecular timescale that we infer when the fossil of *Hypsocephalus* is used to provide a minimum age for the clade “*Lutjanus*” suggests an Early Paleogene origin of the snappers and allies, and of their radiation (~ 62 stem age, ~ 54 Ma crown age). These ages are in fairly good agreement with the Early Eocene estimates for the split between lutjanids and haemulids recovered by large-scale teleost dating analyses (BETANCUR-R. *et al.* 2013; NEAR *et al.* 2013).

It is clear that crown lutjanids had originated by the Middle Eocene, and had already undergone a significant diversification during the Late Eocene and Early Oligocene period. Our results show that a large fraction of the extant lineages originated during this interval. Thus, snappers do not appear to have experienced the same extent of Late Oligocene/Early Miocene radiations that were identified in other reef-associated groups, such as pufferfishes, triggerfishes and allies (ALFARO *et al.* 2007; DORNBURG *et al.* 2011; SANTINI *et al.* 2013a, 2013b), butterflyfishes (COWMAN & BELLWOOD 2011) and parrotfishes (ALFARO *et al.* 2009; KAZANCIÖGLU *et al.* 2009; COWMAN & BELLWOOD 2011).

Diversification of lutjanids

A Yule model with constant rate of speciation may explain the tempo of diversification across the family. However the gamma statistic, the MCCR test and the comparison of lineage diversification models support a slowdown in the diversification rate across the “lutjanins + caesionins” clade (Fig. 3). A shift to accelerated rates of evolution during the early radiation of this major group could explain this clade-specific dynamic.

Figure 2 (opposite page) – BEAST chronogram of lutjanids. Blue bars indicate 95% HPD. The fossil calibration applied to the clade “*Lutjanus*” is indicated by the #1. Fish images modified under Creative Commons license from original photographs by J. E. Randall (retrieved from www.fishbase.org).

The “lutjanins + caesionins” clade includes 75% of the extant diversity of Lutjanidae and groups most of the lutjanids living in shallow waters and reef-associated habitats (NEWMAN & WILLIAMS 1996). As the great majority of studies of modern reef fish families did not recover a signal of slowdown in diversification rate from time-calibrated molecular phylogenies (e.g., COWMAN & BELLWOOD 2011; DORNBURG *et al.* 2011; FRÉDÉRICH *et al.* 2013; but see seabreams and porgies - SANTINI *et al.* 2014), there seems to be evidence that the evolutionary history of this lutjanid subclade may show a different dynamic to that of other coral reef fish groups. While the data presently available do not allow us to more thoroughly test this, we hypothesize that lineages of *Lutjanus* and other closely related genera may have avoided the pattern of severe Oligocene extinctions that probably affected other reef-associated groups (COWMAN & BELLWOOD 2011; BELLWOOD *et al.* 2016). Such extinction avoidance may be due either to some aspects of their ecology or because they were able to occupy some kind of refugia, such as estuarine and brackish areas that many extant species of *Lutjanus* are known to inhabit, at least at the juvenile stage (NAGELKERKEN *et al.* 2000).

An early divergence among macrohabitat specialists could explain the ecological radiation in Lutjanidae, as already suggested for parrotfishes by STREELMAN *et al.* (2002). There is a strong variation of habitat preferences among lutjanids. The first steps of lineage divergence are probably associated with depth segregation: *Randallichthys*, *Aphareus*, *Pristipomoides*, *Etelis* are bottom-dwelling fishes usually encountered below 200 m depth; *Paracaesio* are characteristic of intermediate depth (100–200 m); and the others live in shallow waters less than 100 m (e.g., *Aprion*, *Lutjanus*, *Symphorichthys* and *Symphorus*) (NEWMAN & WILLIAMS 1996; FROESE & PAULY 2016). *Lutjanus* and closely related genera (*Symphorichthys*, *Symphorus*, *Hoplopagrus*) are known to differ in their distribution across the continental shelf (NEWMAN & WILLIAMS 1996), and a review of the available literature on their distribution allowed us to partially illustrate such an ecological radiation. The subclades grouping species of *Lutjanus* are mainly characterized by species living either on the inshore, or the mid shelf or the outer shelf of reef environments. *Lutjanus kasmira* (Forsskål, 1775), *L. bohar* (Forsskål, 1775), *L. fulvus* (Forster, 1801) and *L. quinquelineatus* (Bloch, 1790) form a group of species mainly associated with the outer reef slope (LYTHGOE *et al.* 1994; NEWMAN & WILLIAMS 1996). On the other hand, the clade including *L. sebae*, *L. malabaricus*, *L. erythropterus* groups taxa living in the mid shelf and the inner reef (NEWMAN & WILLIAMS 1996). Moreover, the visual pigments of the species of *Lutjanus*

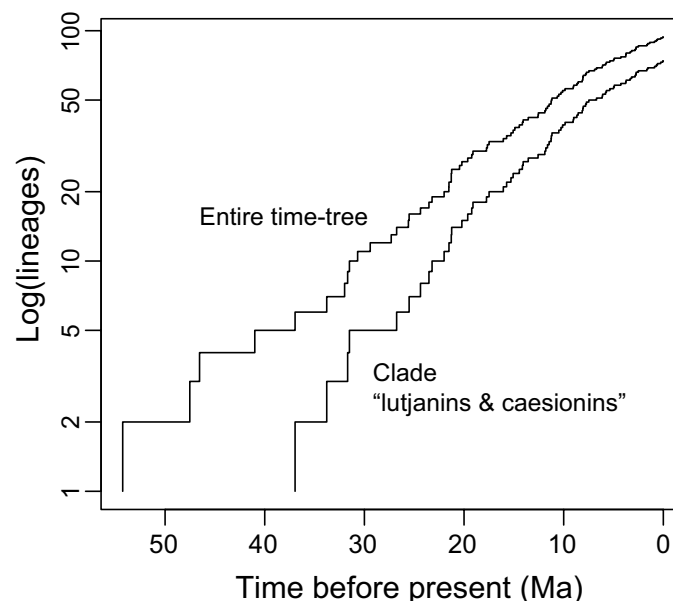


Figure 3 – Lineages through time plot. The figure illustrates the accumulation of lutjanid diversity across the entire tree, as well as the accumulation of lineages within the clade formed by “lutjanins and caesionins”. The number of lineages was log-transformed (y-axis).

living in the clear blue water of the outer reefs differ from their relatives living in “green” and turbid inshore waters (LYTHGOE *et al.* 1994). Directional selection on visual systems could thus have driven an early divergence of macrohabitats in the species of *Lutjanus*, a hypothesis that would clearly require future testing.

The species of *Lutjanus* not only vary in their habitat preference at the adult stage, but also differ in their life history strategies. Indeed, various *Lutjanus* experience ontogenetic habitat shifts (e.g., NAGELKERKEN *et al.* 2000; ABURTO-OROPEZA *et al.* 2009). In some species, juveniles grow in estuaries, mangroves or seagrass beds, then migrate onto adjacent coral reefs (COCHERET DE LA MORINIÈRE *et al.* 2003). In others, the juvenile phase is completed around a reef environment similar to that inhabited by their adults. To date, this ontogenetic trait is still poorly documented for a large number of species represented in our phylogeny but the available data allow us to formulate some hypotheses. The juveniles of the species of *Lutjanus* from clade A (e.g., *L. sebae*, *L. erythropterus* and *L. malabricus*) are rarely encountered in mangrove estuaries (NEWMAN, 1995) while the great majority of the species of *Lutjanus* from clade C frequently complete their juvenile phase in estuaries, mangroves or seagrass beds (LYTHGOE *et al.* 1994; NEWMAN & WILLIAMS 1996; NAGELKERKEN *et al.* 2000; MARTINEZ-ANDRADE 2003; MONTEIRO, *et al.* 2009; PIMENTEL & JOYEUX 2010). This observation suggests a shift to mangrove-, seagrass bed- and estuarine-dependence for the clade C of *Lutjanus*, although this assumption certainly needs further investigations. The turbid waters of these three types of habitats provide a great abundance of food for fishes, and decrease the foraging efficiency of predators (NAGELKERKEN *et al.* 2000). Such ecological factors may boost the fitness of fishes adapted to these environments, such as some species of *Lutjanus*, and ultimately may explain their evolutionary success. The ontogenetic habitat shift observed in *Lutjanus* is also usually associated with diet shifts (COCHERET DE LA MORINIÈRE *et al.* 2003; BERKSTRÖM *et al.* 2013). The relation between habitat and diet shifts could vary among species (BERKSTRÖM *et al.* 2013), reducing competition and allowing coexistence of close relatives.

In addition to habitat partitioning and variation in life history strategies, trophic strategies vary among subclades. Most lutjanids feed on fishes and crabs (ALLEN 1985) but the trophic shift to zooplanktivory observed in Caesioninae could also be responsible for promoting lineage diversification (LOBATO *et al.* 2014). Finally, other factors could sustain speciation. A large body of marine biogeographic literature strongly suggests that allopatric speciation events have certainly had an important role in driving diversification in many reef-associated fishes (SANTINI & WINTERBOTTOM 2002; BRIGGS & BOWEN 2012; LITSIOS *et al.* 2014), and there is no reason to think that snappers were not affected by this phenomenon.

Conclusions

We provide the first densely-sampled molecular phylogeny of Lutjanidae. Our new tree corroborates some of the findings of earlier studies. The caesionins are nested within the lutjanins, suggesting that zooplanktivory evolved from ancestors that had a piscivorous or crustacean-based diet. Several traditional genera, such as the speciose *Lutjanus* that includes over half of the species of snappers, are non-monophyletic. Our time-tree shows that lutjanids most likely separated from their sister group (haemulids) during the Late Cretaceous to Early Paleocene, and subsequently split into two clades during the Paleocene/Early Eocene. Lutjanids experienced significant radiation during the Late Eocene and Early Oligocene, in contrast to a pattern of mostly Late Oligocene/Miocene radiation observed in many other reef-associated groups. Comparative methods indicate a constant rate of speciation across the family but we found some evidence of a variation in the tempo of cladogenesis during the evolution of the major clade “lutjanins and caesionins”. We argue that lutjanids may have experienced an early ecological radiation due to habitat partitioning. Differences in diet and life history strategies have also probably influenced the diversification of the largest clade, formed by lutjanins and caesionins. However additional research combining ecological and morphological data, as well as phylogenetic comparative methods, is clearly needed to test these hypotheses.

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Table S1

List of species included in this study with GenBank accession number of sequences used for phylogenetic analyses.

#	Taxon	<i>16s</i>	<i>cox1</i>	<i>Cytb</i>	<i>Rag1</i>
1	<i>Haemulon sciurus</i> (Haemulidae)	JQ938959	JQ841208	AF240747	JX189823
2	<i>Plectorhinchus orientalis</i> (Haemulidae)	NC_027097	NC_027097	NC_027097	HQ676673
3	<i>Aphareus furca</i>	DQ784722	HQ676753	DQ784746	HQ676633
4	<i>Aphareus rutilans</i>		HQ561493	KU954262	
5	<i>Aprion virescens</i>	DQ784723	JF492869	DQ784747	
6	<i>Apsilus dentatus</i>		HQ162409	HQ162458	
7	<i>Caesio caeruleaurea</i>	DQ784724	GU804898	AF381273	
8	<i>Caesio cuning</i>	DQ784725	KC970453	AF240749	KF141193
9	<i>Caesio lunaris</i>		JQ349804		EU167813
10	<i>Caesio xanthonota</i>		JF492995		
11	<i>Dipterygonotus balteatus</i>		KF489569	AF381270	
12	<i>Etelis carbunculus</i>		EF609353	KF920552	
13	<i>Etelis coruscans</i>		JF493464	KF920529	
14	<i>Etelis oculatus</i>		GU225202	HQ162420	
15	<i>Etelis radiosus</i>		KU954260	KU954277	
16	<i>Gymnocaesio gymnoptera</i>		HQ561514		EU167837
17	<i>Hoplopagrus guentherii</i>		KJ557448	KJ570970	
18	<i>Lutjanus adetii</i>	DQ784727	EF609393	DQ784751	
19	<i>Lutjanus analis</i>	AY857938	JQ842198	HQ162432	EF095662
20	<i>Lutjanus apodus</i>	JQ741057	GU225357	HQ162435	
21	<i>Lutjanus aratus</i>		KJ557442	KJ570964	
22	<i>Lutjanus argentimaculatus</i>	DQ784728	JF493820	EF025494	EU627659
23	<i>Lutjanus argentiventris</i>	AY947839	GU440385	KJ570955	
24	<i>Lutjanus bengalensis</i>	FJ171339	FJ171339	FJ171339	EU627660
25	<i>Lutjanus biguttatus</i>		KF009607		JX189829
26	<i>Lutjanus bitaeniatus</i>		KC130849		
27	<i>Lutjanus bohar</i>	DQ784729	JF952787	DQ784753	
28	<i>Lutjanus bouton</i>		KT718540		
29	<i>Lutjanus buccanella</i>		JQ842205	HQ162438	
30	<i>Lutjanus campechanus</i>	AY857940	HQ162373	AY374294	
31	<i>Lutjanus carponotatus</i>	DQ78473	EF609395	DQ784754	
32	<i>Lutjanus colorado</i>	HQ127652	GU186970	KJ570961	

#	Taxon	16s	cox1	Cytb	Rag1
33	<i>Lutjanus cyanopterus</i>		GQ329867	HQ162441	
34	<i>Lutjanus decussatus</i>	AF247445	KC130837	AF240750	
35	<i>Lutjanus dentatus</i>				EU167846
36	<i>Lutjanus ehrenbergii</i>		HQ149873		
37	<i>Lutjanus erythropterus</i>	GQ265897	GQ265897	GQ265897	EU627661
38	<i>Lutjanus fulviflamma</i>	DQ784731	JF493832	EF376177	EU627662
39	<i>Lutjanus fulvus</i>	DQ784732	JQ431896	AY501366	EU627672
40	<i>Lutjanus gibbus</i>	DQ784733	GU805121	DQ784757	
41	<i>Lutjanus griseus</i>	AY857944	GU225643	HQ162426	KF141274
42	<i>Lutjanus guttatus</i>		KJ557427	KJ570949	
43	<i>Lutjanus indicus</i>		KF830923		
44	<i>Lutjanus inermis</i>		KJ557430	KJ570952	
45	<i>Lutjanus jocu</i>	AY857943	FJ998476	HQ162444	
46	<i>Lutjanus johnii</i>	KJ643926	KJ643926	KJ643926	EU627663
47	<i>Lutjanus kasmira</i>	FJ416614	FJ416614	FJ416614	EU627664
48	<i>Lutjanus lemniscatus</i>		EF609397		
49	<i>Lutjanus lutjanus</i>		FJ237812		EU627665
50	<i>Lutjanus madras</i>		JN208427		
51	<i>Lutjanus mahogoni</i>		GU225372	HQ162445	EU182625
52	<i>Lutjanus malabaricus</i>	FJ824741	FJ824741	FJ824741	EU627666
53	<i>Lutjanus monostigma</i>	DQ784735	KC130845	DQ784759	
54	<i>Lutjanus notatus</i>		HQ561531	KJ570959	
55	<i>Lutjanus novemfasciatus</i>	AY958620	GU440386	KJ570965	
56	<i>Lutjanus ophuysenii</i>		EU600098	EF376179	EU627671
57	<i>Lutjanus papuensis</i>		HM422401		
58	<i>Lutjanus peru</i>	AY947840	HQ162412	HQ162461	
59	<i>Lutjanus purpureus</i>	KJ907227	JX297373		KJ907361
60	<i>Lutjanus quinquelineatus</i>	DQ784736	JF952789	DQ784760	
61	<i>Lutjanus rivulatus</i>		JF493845	DQ484045	
62	<i>Lutjanus russellii</i>	EF514208	EF514208	EF514208	EU627667
63	<i>Lutjanus sanguineus</i>		JF493850	DQ484049	JN106042
64	<i>Lutjanus sebae</i>	FJ824742	FJ824742	FJ824742	EU627668
65	<i>Lutjanus stellatus</i>	DQ444483	EU600133	EF376163	EU627670
66	<i>Lutjanus synagris</i>	AY857939	GU225376	HQ162429	
67	<i>Lutjanus timoriensis</i>		KJ202176		

#	Taxon	16s	cox1	Cytb	Rag1
68	<i>Lutjanus viridis</i>		KJ557434	KJ570956	
69	<i>Lutjanus vitta</i>	DQ784739	EF609402	EF376181	EU627669
70	<i>Lutjanus vivanus</i>		HQ162397	HQ162448	
71	<i>Lutjanus xanthopinnis</i>		LC071442		
72	<i>Macolor macularis</i>		KF930094		
73	<i>Macolor niger</i>	DQ784740	KF489639	DQ784764	
74	<i>Ocyurus chrysurus</i>	AY857942	FJ998488	HQ162451	JX189830
75	<i>Paracaesio sordida</i>		GU805104		
76	<i>Paracaesio xanthura</i>		JF494063		
77	<i>Pinjalo lewisi</i>		KP856802	KR007727	
78	<i>Pinjalo pinjalo</i>		JN208390		EU167860
79	<i>Pristipomoides aquilonaris</i>	DQ532943	HQ162403	HQ162457	
80	<i>Pristipomoides argyrogrammicus</i>		KF930322		
81	<i>Pristipomoides auricilla</i>		JQ432043		
82	<i>Pristipomoides filamentosus</i>		DQ885120	JQ083093	
83	<i>Pristipomoides multidentis</i>	KF430626	KF430626	KF430626	
84	<i>Pristipomoides sieboldii</i>		GU805046		
85	<i>Pristipomoides typus</i>		EF609438		
86	<i>Pterocaesio chrysozona</i>		JQ350291		
87	<i>Pterocaesio digramma</i>	LC099463	KF009653		
88	<i>Pterocaesio marri</i>	DQ784742	GU804914	DQ784766	
89	<i>Pterocaesio pisang</i>	DQ784743	KJ202192	DQ784767	KF141343
90	<i>Pterocaesio tessellata</i>		KJ202193		
91	<i>Pterocaesio tile</i>	AP004447	AP004447	AP004447	
92	<i>Pterocaesio trilineata</i>		HQ561504		
93	<i>Randallichthys filamentosus</i>		KP954301		
94	<i>Rhomboplites aurorubens</i>	AY857941	HQ162406	AY294198	KF141349
95	<i>Symphorichthys spilurus</i>	DQ784744	FJ584135	DQ784768	
96	<i>Symphorus nematophorus</i>	DQ784745	KC130829	DQ784769	EU167876