
1 A Phylogenetic Context

The Diversification of Damselfishes (Pomacentridae)

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1.1 INTRODUCTION

Damselfishes (Teleostei: Pomacentridae) represent a species-rich group of primarily marine fishes (rare in brackish water). They are distributed worldwide, inhabiting coastal habitats of tropical and temperate seas, and they represent a major component of reef communities (rocky and coral reefs) (Allen 1991; Frédérich and Parmentier 2016). In August 2021, Eschmeyer's catalog of fishes referred to 424 valid damselfish species distributed in four subfamilies and 29 genera (Table 1.1) (Eschmeyer et al. 2021; Tang et al. 2021). New species are still regularly described, as demonstrated by the description of approximately three species per year during the last ten years (Eschmeyer et al. 2021). The diagnosis of damselfish is provided in Parmentier and Frédérich (2016). In this chapter devoted to the diversity of damselfishes (Figure 1.1), I will first highlight two ecological specializations only present in Pomacentridae. Then, I will aim (a) to discuss the phylogenetic position of damselfishes within the ray-finned fishes (Actinopterygii), (b) to summarize the recent advances in the systematics of damselfishes, and (c) to describe the pattern of ecological diversification observed in damselfishes.

1.2 FARMERS AND CLOWNFISHES: UNIQUENESS OF DAMSELFISHES AMONG RAY-FINNED FISHES

The Pomacentridae are a highly diverse group of reef fishes, especially regarding their diversity of ecology, morphology, and behavior (Allen 1991; Frédérich and Parmentier 2016). The Pomacentridae include solitary and gregarious species (Fishelson 1998). The majority of solitary species are highly territorial, defending a small area against intruders such as fishes and mobile invertebrates. Some of these

territorial damselfishes are considered algal farmers, cultivating and protecting distinct crop assemblages (Hata and Kato 2004; Ceccarelli et al. 2005). As reviewed by Hata and Ceccarelli (2016), damselfishes manage their farms in at least three ways. Firstly, territorial defence alters herbivory that occurs inside territories, leading to an algal assemblage which differs from that found outside territory boundaries. Secondly, damselfishes prepare substratum for their farm by, for example, killing corals, and they also invest in farm maintenance by “cleaning up” debris from their territory. Finally, fish selectively remove unpalatable algae to promote the growth of their preferred algae (i.e., weeding behavior). The types of algal farms vary among territorial damselfishes: there is a continuum between some species producing intensive monoculture of palatable algal species on a small territory (e.g., *Stegastes nigricans*) and others managing extensive mixed-culture of algae on a larger territory (e.g., *Stegastes obreptus*). Cultivation of algae was also reported for limpets (Branch 1981) and some herbivorous cichlids (Hata et al. 2014) but the farming behavior of damselfishes appear to be the most advanced in aquatic environments, even leading to obligate plant-herbivore cultivation mutualism (Hata and Kato 2006). Farming behavior evolved multiple times during the evolutionary history of damselfishes (Frédérich et al. 2013; McCord et al. 2021) and the research on damselfish adaptations related to farming is currently ongoing (Olivier et al. 2014, 2016a, 2021).

The gregarious damselfishes show diverse social structures, including species with either monogamous or polygamous adults (Fishelson 1998). The best examples of monogamous pomacentrid species are the brightly colored clownfishes (*Amphiprion* spp.), which form permanent reproductive pairs with a high level of fidelity. Beyond this, the clownfishes, a monophyletic lineage within Pomacentridae (Litsios et al. 2012b), are well known for

TABLE 1.1
List of Subfamilies, Tribes, and Genera Following the
New Taxonomic Classification of Pomacentridae

Subfamily	Tribes	Genus	N	
Microspathodontinae		<i>Hypsypops</i>	70	
		<i>Lepidozygus</i>		
		<i>Mecaenichthys</i>		
		<i>Microspathodon</i>		
		<i>Nexilosus</i>		
		<i>Parma</i>		
		<i>Plectroglyphidodon</i>		
		<i>Similiparma</i>		
		<i>Stegastes</i>		
	Glyphisodontinae			<i>Abudfeduf</i>
Chrominae		<i>Azurina</i>	122	
		<i>Chromis</i>		
		<i>Dascyllus</i>		
		<i>Pycnochromis</i>		
Pomacentrinae	Amphiprionini	<i>Amphiprion</i>	211	
		<i>Cheiloprion</i>		
	Cheiloprionini	<i>Chrysiptera sensu stricto</i>		
		<i>“Chrysiptera”</i>		
		<i>Dischistodus</i>		
		<i>Pomachromis</i>		
		Hemiglyphidodontini		<i>Acanthochromis</i>
				<i>Altrichthys</i>
				<i>Amblyglyphidodon</i>
	<i>Hemiglyphidodon</i>			
	Pomacentrini	<i>Neoglyphidodon</i>		
		<i>Amblypomacentrus</i>		
		<i>Neopomacentrus</i>		
		<i>Pomacentrus</i>		
		<i>Pristotis</i>		
				<i>Teixeirichthys</i>

Source: Tang et al. (2021).

their symbiosis with tropical sea anemones that was first reported in 1868 (Collingwood 1868). This intimate relationship, unique in the animal kingdom, has become a textbook example of mutualistic interactions (Fautin 1986, 1991) and a great deal of attention has been given to this symbiosis. As witnessed by the present book, research about the biology of clownfishes is ongoing in many areas.

1.3 PHYLOGENETIC POSITION OF DAMSELFISHES WITHIN RAY-FINNED FISHES (ACTINOPTERYGII)

With more than 30,000 species, the ray-finned fishes (actinopterygians) represent one of the most successful radiations in the history of vertebrates. The great majority of

actinopterygians (99.8%) are teleost fishes (Nelson et al. 2016) and among this species-rich clade, Müller (1843) distinguished a taxon called Pharyngognathi acanthopterygii with the following traits: (1) the lower pharyngeal bones are coalesced forming jaws; (2) part of the rays of the dorsal, anal, and ventral fins are not articulated forming spines; and (3) the swim bladder is deprived of a pneumatic duct. As synthesized by Parmentier and Frédérick (2016), the Pomacentridae (Labroidei ctenoidei *sensu* Müller) was one of the first families constituting this order made by Müller (1843, 1844) with cichlids (Cichlidae) and labrids (Labridae).

The possession of pharyngeal jaw apparatus, or “pharyngognathy”, and associated morphological characteristics were studied and used as systematic characters (Müller 1843; Stiassny 1981; Stiassny and Jensen 1987). As currently recognized, pharyngognathy involves three prominent modifications to the typical pharyngeal jaw apparatus of percomorphs: (1) left and right lower jaw elements (fifth ceratobranchials) that are united to make a single lower pharyngeal jaw; (2) a muscular sling that directly connects the underside of the neurocranium with the lower pharyngeal jaw; and (3) a mobile diarthrotic articulation of the upper pharyngeal jaws with the neurocranium (Stiassny 1981; Stiassny and Jensen 1987; Wainwright et al. 2012). These morphological and functional features were proposed as synapomorphies uniting the Labroidei clade that included Cichlidae, Embiotocidae, Labridae, Odacidae, Scaridae, and Pomacentridae (Liem and Greenwood 1981; Kaufman and Liem 1982). In parallel to an interest in systematics, this fascinating system of pharyngeal jaws was deeply studied from a functional point of view (Liem 1973; Liem and Osse 1975). Liem argued that the acquisition of an extra set of jaws in cichlids and other Labroidei has enabled a diversification of food preparation techniques and therefore feeding habits (Liem 1973; Liem and Osse 1975; Liem and Greenwood 1981). First, the flexibility of this highly integrated pharyngeal jaw apparatus would be a major factor that has enabled this diversity of feeding habits. Then, such a duplication of jaws (oral and pharyngeal jaws) was viewed as an evolutionary novelty leading to the functional decoupling between prey capture and prey processing (Liem 1973; Hulsey 2006), ultimately allowing the independent morphological diversification of both jaws systems. The functional morphology of pharyngeal jaws apparatus varies among Labroidei lineages (Stiassny and Jensen 1987; Wainwright et al. 2012). In damselfishes, the characteristics of the lower pharyngeal jaw (LPJ) are a Y-shape (and width is greater than the length), no trace of a central sutural union, a well-developed median keel on the ventral face of the bone, and tooth rows arranged radially across the LPJ with teeth located over the median region of the jaw (Kaufman and Liem 1982; Stiassny and Jensen 1987). Although it is not found in all the pomacentrids (e.g., *Microspathodon* and *Chromis*), pharyngo-cleithral articulations can join the expanded lateral horns of the LPJ to the cleithrum (Liem 1973; Liem and Greenwood 1981; Stiassny and Jensen 1987). It is expected that the support



FIGURE 1.1 Sample of eight species illustrating damselfish diversity. Photos were gratefully provided by Florent Charpin (*Stegastes*, *Abudefduf*, *Chromis*, and *Dascyllus* – reefguide.org) and Mark Erdmann (*Amphiprion*, *Amblyglyphidodon*, *Pomacentrus*, and *Chrysiptera*).

provided by the articulation of the LPJ with the shoulder girdle increases the total biting force that can be exerted on prey (Galis and Snelderwaard 1997).

Our knowledge of the phylogeny of ray-finned fishes has significantly advanced in recent years thanks to the

phylogenetic analyses including many genes, morphological characters and fossil data (e.g., Near et al. 2012; Broughton et al. 2013; Faircloth et al. 2013; Chen et al. 2014; Davesne et al. 2016; Betancur et al. 2017; Alfaro et al. 2018; Hughes et al. 2018). Among other advances

in our understanding of the evolution of ray-finned fishes, molecular phylogenetic studies revealed polyphyly of the traditional clade of Labroidei and thus showed that pharyngognathy evolved multiple times during the radiation of actinopterygians (Mabuchi et al. 2007; Wainwright et al. 2012). Labridae (including odacines and scarines which are nested within Labridae (Bellwood 1994; Clements et al. 2004; Westneat and Alfaro 2005) are separated from the remainder of the traditional labroid lineages (Cichlidae, Embiotocidae, and Pomacentridae). These three families are now included in a clade of 40 families and more than 4,800 species which were named Ovalentaria (taxonomic level: series) for their characteristic demersal, adhesive eggs with chorionic filaments (Wainwright et al. 2012; Betancur et al. 2017). In addition to cichlids, damselfishes, and surfperches, Ovalentaria includes familiar lineages of fishes such as blennies, silversides, dottybacks, and mullets. If the monophyly of Ovalentaria is strongly supported, interrelationships among the major lineages of Ovalentaria are still not well-resolved (Wainwright et al. 2012; Eytan et al. 2015). To date, there is no consensus about which lineage is the most closely related to Pomacentridae.

One major anatomical characteristic of damselfish is the cerato-mandibular ligament (c-md) that joins the ceratohyal of the hyoid bar to the lower jaw, at the level of the coronoid process (Stiassny 1981; Olivier et al. 2016a) (Figure 1.2). Although secondarily lost in some species (Frédérich et al. 2014), this ligament appears to be a synapomorphic trait within Pomacentridae (Stiassny 1981). Recent works have highlighted that the c-md is involved in at least two major functions of damselfish behavior: sound production (Parmentier et al. 2007; Colleye et al. 2012) and feeding (Olivier et al. 2015, 2016b). Both behaviors are based on the same principle: the c-md allows rapidly closing the lower jaws in a few milliseconds, without the help of the *adductor mandibulae* muscles. The slam of the oral jaws causes teeth collision creating a vibrational wave and the resulting sounds (Colleye et al. 2012). Olivier et al. (2021) recently demonstrated that the possession of two mouth-closing systems enabled grazing damselfishes to have a forceful and extremely fast bite, challenging thus the functional trade-off between force and velocity. Currently, it is hypothesized that the cmd would have operated as a fundamental key to the process of diversification in damselfishes (Frédérich et al. 2014; Olivier et al. 2016a, 2021). According to the expected importance of the cmd, Olivier et al. (2016a) checked the presence of such a ligament in eight groups of Ovalentaria. Only Pomacentridae and Pseudochrominae share the presence of a cmd ligament but its insertion differs between the two groups, suggesting a difference in its function (Olivier et al. 2016a). Conversely to a potential morphological link between Pomacentridae and Pseudochrominae, Tang et al. (2021) provided molecular data supporting the hypothesis that the Embiotocidae would be the sister group of Pomacentridae. Regarding these conflicting results (Eytan et al. 2015; Olivier et al. 2016a; Tang et al. 2021), additional works concerning the identity of the damselfish sister group are clearly needed.

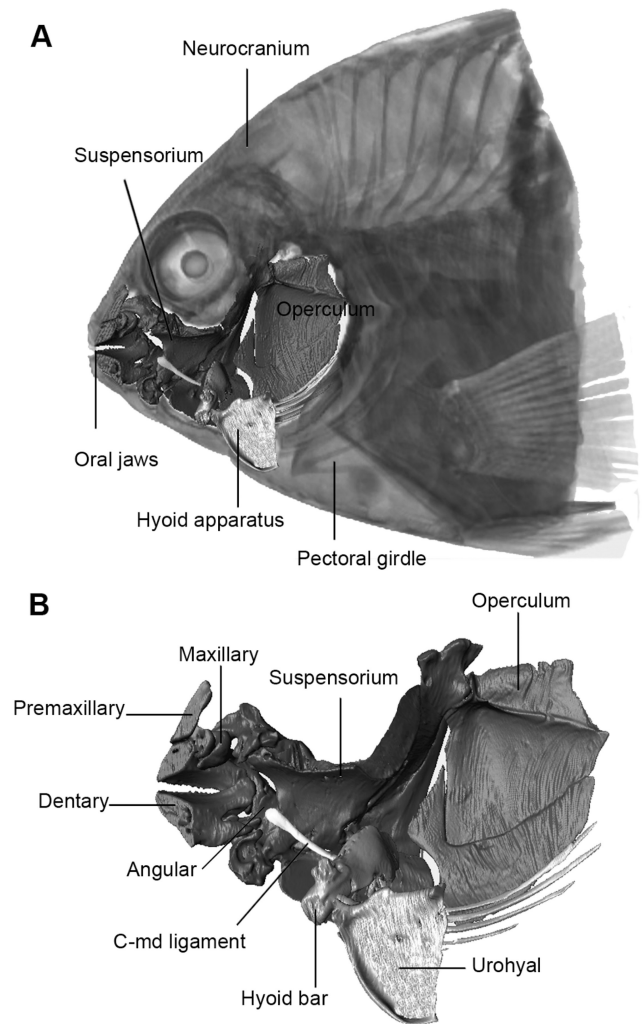


FIGURE 1.2 Illustration of the cerato-mandibular (c-md) ligament in damselfishes. (A) Left lateral view of *Stegastes rectifraenum*. The left oral jaw, suspensorium, opercle, and hyoid bar have been removed allowing view of the right part of the hyoid apparatus in the buccal cavity. The cerato-mandibular ligament is highlighted in green on this 3-D reconstruction. (B) Zoom on the 3-D reconstruction.

1.4 SYSTEMATICS OF DAMSELFISHES

The family Pomacentridae is monophyletic. Recent phylogenies of damselfishes, mostly based on DNA sequence data, agree with the presence of four major clades reflecting the current taxonomic classification with four subfamilies: Microspathodontinae, Chrominae, Glyphosodontinae, and Pomacentrinae (Cooper et al. 2009; Cooper and Santini 2016; McCord et al. 2021; Tang et al. 2021). The systematics of damselfishes was reviewed by Cooper and Santini (2016) and even more recently by Tang et al. (2021) and McCord et al. (2021). Here, I briefly summarize these two most exhaustive studies providing phylogenetic hypotheses with the largest taxon sampling (322 and 345 species) (Figure 1.3). Discordances between these two studies built on different numbers of traditional Sanger loci (5 mtDNA & 3 nuDNA in Tang et al. [2021]; 7 mtDNA & 5 nuDNA in

McCord et al. [2021]) will be pointed out but further details can be found within.

The subfamily Microspathodontinae, including nine genera (Table 1.1), is the sister group of all other pomacentrids (Figure 1.3). This clade includes the largest damselfishes with *Parma* species living around Australia and New Zealand (>200 mm of standard length) and the tribe Microspathodontini, the so-well named “giant damselfishes” (i.e., *Hypsipops*, *Nexilosus*, *Similiparma*, and *Microspathodon* [>300 mm SL]) (Cooper and Santini 2016) which are confined to the Atlantic and Eastern Pacific. Both

Plectroglyphidodon and *Stegastes* are not monophyletic. A clade including the great majority of *Plectroglyphidodon* species and some *Stegastes* appears to be the sister lineage to Microspathodontini. Accordingly, Tang et al. (2021) suggested classifying this first group of “*Stegastes*” as *Plectroglyphidodon*. The monotypic *Lepidozygus* is the sister lineage of a clade made by the rest of *Stegastes* species and *Plectroglyphidodon lacrymatus*. Then Tang et al. (2021) referred now to *Stegastes lacrymatus*.

The subfamily Glyphisodontinae is made of the genus *Abudefduf*, which includes 21 species. On one hand, Tang

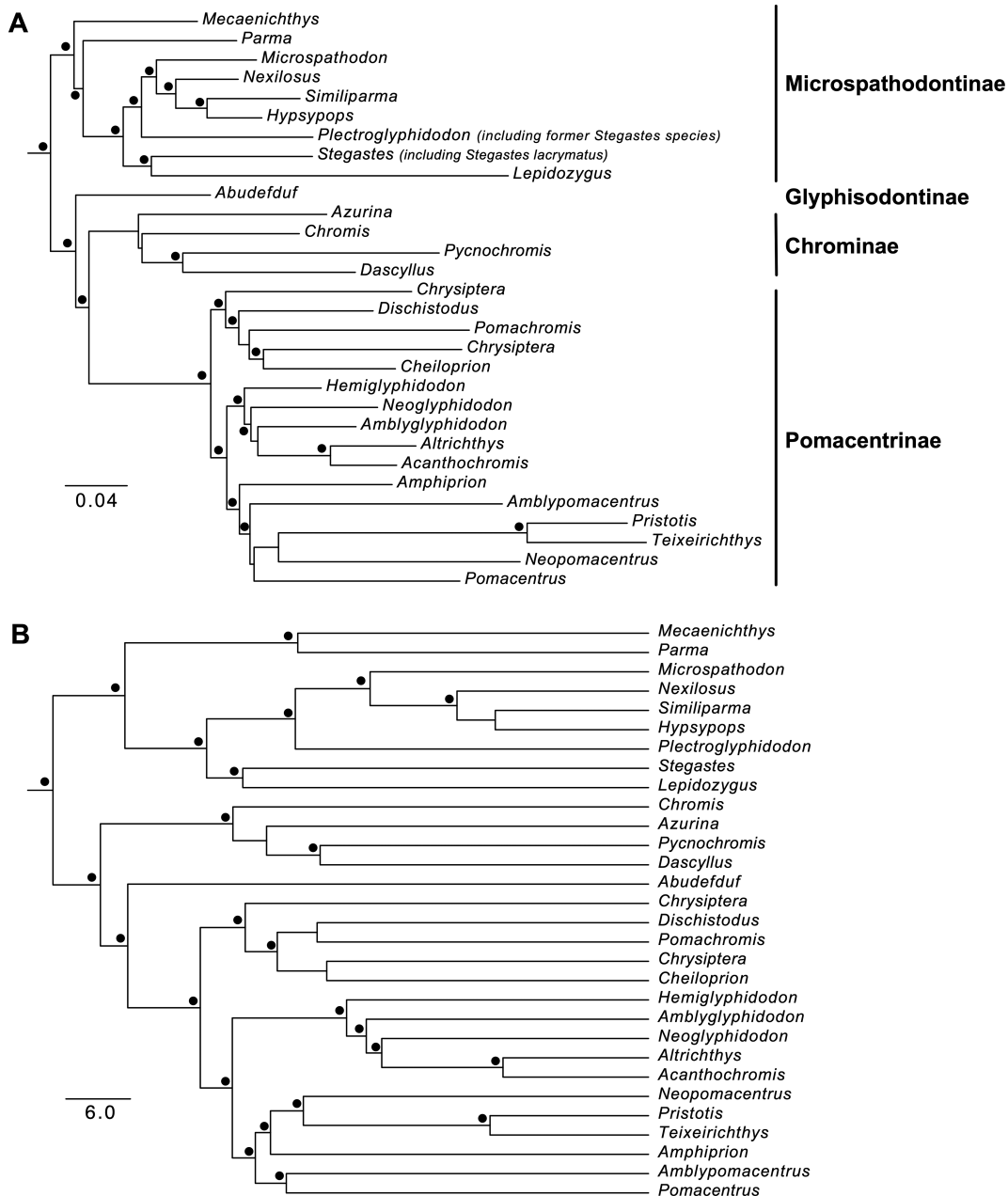


FIGURE 1.3 (A) Maximum likelihood topology of the molecular phylogeny from Tang et al. (2021) and (B) time-calibrated topology of the phylogeny from McCord et al. (2021) illustrating the relationships among the recognized genera of damselfishes. Bootstrap support values greater than 90% and nodal values with Bayesian posterior support levels above 0.9 are indicated with black dots on (A) and (B), respectively.

et al. (2021) retrieved this monophyletic group as a sister to a clade formed by the subfamilies Chrominae and Pomacentrinae. On the other hand, the analyses of McCord et al. (2021) support Glyphisodontinae as the sister group of Pomacentrinae. Such disagreement is not new (see discussion in Tang et al. 2021) and the exact position of Glyphisodontinae is still unresolved (Figure 1.3).

The subfamily Chrominae, including four genera (Table 1.1), appears as the sister group to the subfamily Pomacentrinae in the phylogeny of Tang et al. (2021). Conversely, in McCord et al. (2021)'s phylogeny, Chrominae are sisters to a clade formed by the subfamilies Glyphisodontinae and Pomacentrinae. The Chrominae is dominated by representatives of the polyphyletic genus *Chromis*, which are currently distributed in three disjunct clades. Tang et al. (2021) solved this polyphyly by breaking up the putative *Chromis* species into three different genera: species most closely related to *Azurina hirundo* are now referred to as *Azurina* (e.g., *Chromis cyanea* becomes *Azurina cyanea*), species forming the sister clade of *Dascyllus* are now referred to as *Pycnochromis*, and the other species fall into the clade of *Chromis sensu stricto*. The tree topology of McCord et al. (2021) agrees with this except for a small group of *Chromis* that are outside the main group.

The Pomacentrinae is the largest subfamily, grouping 15 of the 29 genera and holding half of all currently recognized species. This subfamily is divided into four tribes by Tang et al. (2021): Amphiprionini, Cheiloprionini, Hemiglyphidodontini, and Pomacentrini. The Cheiloprionini are the sister tribe to the remainder of the subfamily. The Amphiprionini is the tribe grouping all the clownfishes, constituted of the genera *Premnas* and *Amphiprion*. Based on their robust phylogenetic data and earlier studies, Tang et al. (2021) treat *Premnas* as a junior synonym of *Amphiprion*. Thus, *Amphiprion biaculeatus* should be recognized as the valid species. Among other genera (Table 1.1), the Pomacentrini includes the genus *Pomacentrus* which becomes the largest genus in the family (81 species) after the restructuration of the polyphyletic *Chromis* (108 species) (Eschmeyer et al. 2021). The phylogenetic analyses of McCord et al. (2021) identified five clades in Pomacentrinae, which are partially concordant with the ones of Tang et al. (2021), but some nodes were only weakly supported in both analyses.

Fossil records of damselfish are scarce, which is limited to six described taxa unquestionably assigned to Pomacentridae (Cooper and Santini 2016; Cantalice et al. 2020). The earliest record of the family dated from the Paleocene (*Chaychanus gonzalezorum*, 63 million years ago: mya) (Cantalice et al. 2020). Three fossil taxa are from the deposits of Monte Bolca in Italy (Middle Eocene, 50 mya) and two others dated from the Miocene (Cooper and Santini 2016). Currently, no fossil clownfish was found and described. Further details about the damselfish fossil records are available in Bellwood and Sorbini (1996), Carnevale and Landini (2000), Cooper and Santini

(2016), and Cantalice et al. (2020). Fossil data combined with the estimation of the tempo of lineage diversification provided by time-calibrated phylogenies (Litsios et al. 2012a; Frédérich et al. 2013; McCord et al. 2021) suggest that the early diversification of damselfishes occurred just after the Cretaceous-Paleogene boundary (66 mya). The lineages leading to the four extant subfamilies originated during the Eocene and then observed major diversification events during the Miocene-Oligocene (Figure 1.4). Dates of origin and estimates of divergence times for damselfish lineages are detailed in McCord et al. (2021). Briefly, the Microspathodontinae diverged from other pomacentrids at 55 mya and the subclade of giant damselfishes (Microspathodontini) began to diversify ~26 mya. The Chrominae originated 51 mya and extant lineages diverged ~38 mya. Within Chrominae, *Dascyllus*, *Chromis*, and *Pycnochromis* radiated mainly during the Miocene. The Glyphisodontinae diverged from the Pomacentrinae ~49 mya and living *Abudefduf* began to diversify ~31 mya. Major subclades of Pomacentrinae diverge from each other between ~42 and ~34 mya. The diversification of the species-rich group of *Pomacentrus* occurred during the last ~27 million years. The tribe Amphiprionini is relatively young (Litsios et al. 2012b; Frédérich et al. 2013), and according to McCord et al. (2021), it diverged from a common ancestor ~18 mya. Most clownfish species arise only 3–5 mya (Figure 1.4).

1.5 ECOLOGICAL RADIATION OF DAMSELFISHES

With 424 species, the Pomacentridae are an example of a highly successful adaptive radiation. The pomacentrids present a large diversity of habitat use, feeding, morphology, behavior, and color pattern (Frédérich and Parmentier 2016), and resource partitioning is certainly one of the key factors of the process of diversification in damselfishes.

Meekan et al. (1995), Ormond et al. (1996), Pratchett et al. (2016), and Komyakova et al. (2019) are a few examples of detailed comparative analyses of habitat uses in damselfishes. Most of the tropical species live amongst living or dead coral formations on the barrier reef (outer reef slope, reef flat) and in the lagoon (micro-atolls, coral heads, fringing reef). The habitat of numerous species can be restricted to one zone. For example, *Chrysiptera annulata* (*Amblypomacentrus annulatus sensu* [Tang et al. 2021]) lives only on the reef flat of the Great Reef of Toliara in Madagascar (Lepoint et al. 2016). *Stegastes nigricans* and *Dascyllus aruanus* occur strictly in the lagoon (Meekan et al. 1995; Lecchini and Galzin 2005; Gajdzik et al. 2016). On the other hand, some species can be encountered both on the barrier reef and in the lagoon: *Pomacentrus wardi* at Heron Island (Robertson and Lassig 1980) and *Dascyllus flavicaudus* at Moorea Island (Gajdzik et al. 2016). The distribution of the species at small spatial scales is mainly related to the depth, the presence/absence of conspecific,

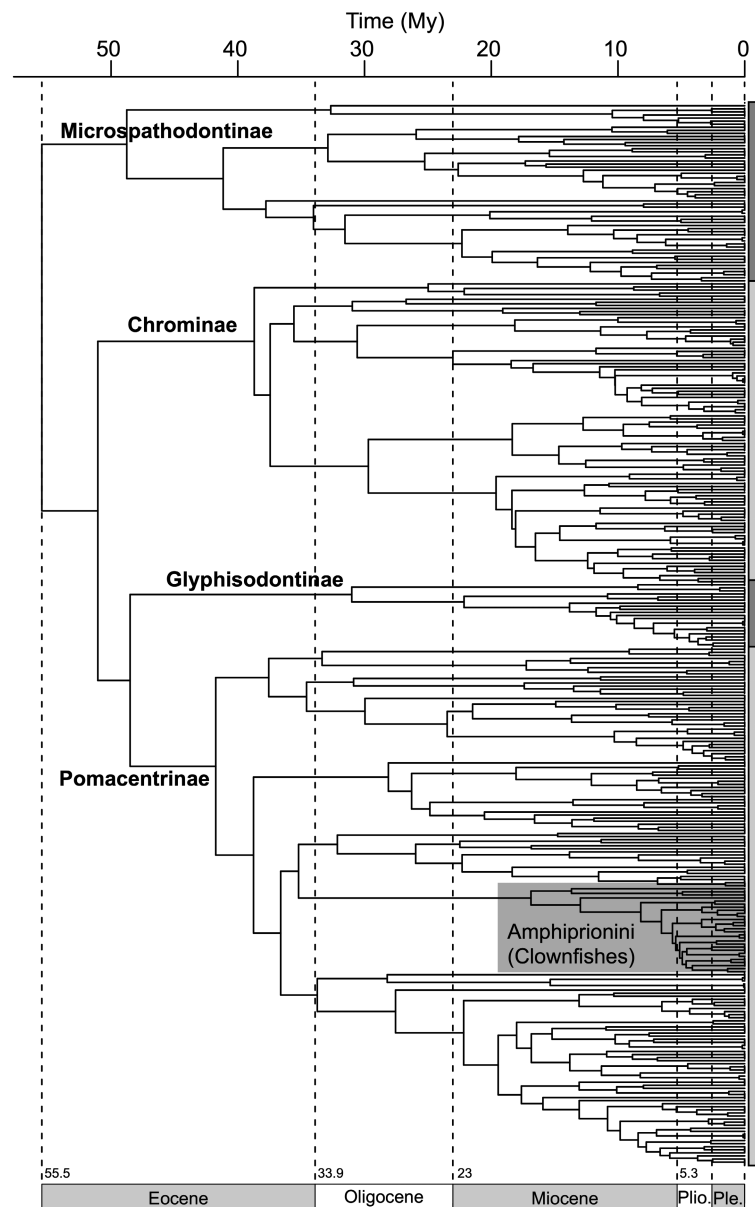


FIGURE 1.4 Consensus time tree from McCord et al. (2021) showing lineage diversification in damselfishes. The four subfamilies and the tribe of clownfishes are identified.

the presence/absence of predators, the coral cover, and/or the kind of substrates (Pratchett et al. 2016; Komyakova et al. 2019). It is worth noting that, among the diversity of habitats available in the tropical coastal environment, relatively few pomacentrids are encountered around mangroves and seagrass beds at the adult stage. For example, *C. annulata* lives in subtidal seagrass meadows found on the reef flat of Toliara Reef (Lepoint et al. 2016) and the presence of some species of the genus *Dischistodus* was reported in a seagrass bed of a fringing reef at Iriomote Island, Southern Japan (Nakamura et al. 2003). In temperate seas, the damselfishes mainly occur in rocky areas (e.g., *Chromis chromis* in the Mediterranean Sea) but some live closely associated with kelp forests (e.g., *Hypsypops rubicundus* along the coast of California) (Allen 1991). Ontogenetic habitat shifts

are present in damselfishes but it is relatively uncommon (Komyakova et al. 2019).

The trophic diversity of damselfishes was extensively studied by *in situ* observations of feeding events, the analyses of stomach contents, and the use of trophic markers such as stable isotopes and fatty acids (reviewed in Frédérich et al. 2016b). Damselfishes may be grouped into three main trophic guilds, established on functional demands, and referring to what and where the prey is caught (Frédérich et al. 2009): (1) the pelagic feeders that feed mainly on planktonic copepods, (2) the benthic feeders that mainly graze on filamentous algae, and (3) an intermediate group including species that forage for their prey in the pelagic and benthic environments in variable proportions (e.g., planktonic and benthic copepods,

small vagile invertebrates, and filamentous algae). At least three damselfishes are known to be corallivorous species: *Cheiloprion labiatus*, *Plectroglyphidodon johnstonianus*, and *Plectroglyphidodon dickii* (Allen 1991; Kuo and Shao 1991; Ho et al. 2009), and may be grouped within the benthic feeders. The division among these three main trophic guilds is not strict. Indeed, a continuum exists between exclusive zooplankton feeders and algivorous species, and it can be difficult to precisely assign some species to one of the three categories due to feeding plasticity (Frédérich et al. 2016b).

Interestingly, dietary specializations, habitat uses, and social behaviors are tightly associated in damselfishes. As observed in the damselfish assemblage of the reef at Moorea Island (Gajdzik et al. 2016), most of the pelagic feeders form large aggregations (either shoals or schools) up to 20 m depth, live in areas bathed by the open ocean or just behind the barrier reef crest, and are associated with live or dead corals. Benthic feeders mostly display territorial, solitary behavior, and they can establish their shelter on various types of substrates. Species from the intermediate group are generally gregarious and forage in protected areas at usually shallower depths than pelagic feeders.

Beyond the study of niche partitioning among sympatric damselfish species from different regions, the evolution of their ecological diversity was also studied at the genus and the family levels (Cooper and Westneat 2009; Aguilar-Medrano 2013, 2017; Frédéricich et al. 2013, 2016a; Aguilar-Medrano and Barber 2016; Gajdzik et al. 2019; McCord et al. 2021). Since the 1970s, numerous ecomorphological studies revealed interspecific variation in various morphological functional traits and discussed their adaptive significance (reviewed in Frédéricich et al. 2016b). Head shape, oral jaws, pharyngeal jaws, oral and pharyngeal teeth, gill rakers, and intestine length all appeared to be ecologically relevant traits allowing the discrimination of the three damselfish feeding guilds. The study of body form and pectoral fins also allowed the discrimination of functional groups related to habitat partitioning and swimming mode (Frédérich et al. 2016a).

The combination of ecological and morphological data with various phylogenetically informed comparative analyses has demonstrated high rates of evolutionary change in the trophic ecology of damselfishes (Cooper and Westneat 2009; Frédéricich et al. 2013; Gajdzik et al. 2019; McCord et al. 2021). What is unusual about this radiation is that instead of invading a large diversity of ecological niches, it has progressed by rapidly and repeatedly converging on similar ecomorphological states (ecotypes). Cooper and Westneat (2009) refer to this pattern as “reticulate adaptive radiation”. Frédéricich et al. (2013) who confirmed this evolutionary pattern with additional species and using other phylogenetic comparative methods, preferred the term “iterative evolution”. Both refer to the repetitive occurrence of similar morphologies, ecologies, or behaviors during the evolutionary progression of a lineage. This pattern of repeated convergence was already described for overall skull shape

(Cooper and Westneat 2009; Aguilar-Medrano et al. 2011), bite mechanics (Cooper and Westneat 2009), oral jaws (Frédérich et al. 2013), farming behavior, and trophic ecology (Cooper and Westneat 2009; Frédéricich et al. 2013), but it is highly expected that other phenotypic traits evolve along the same pattern. One of the ecological outcomes of this evolutionary pattern is the production of highly similar damselfish assemblages in different geographic regions. Even if the number of species varies among regions, Gajdzik et al. (2018) showed consistent levels of eco-functional diversity in coral reef damselfish assemblages in Toliara reef (Madagascar), Dongsha atoll (Taiwan), and Moorea Island (French Polynesia). Every damselfish assemblage, mainly driven by niche-related processes, hosted species whose niches were highly differentiated and evenly distributed in eco-functional spaces (Gajdzik et al. 2018).

Beyond the picture of an iterative ecomorphological radiation, it appears that the pattern of transitions between ecotypes (i.e., the three trophic states: benthic feeder, intermediate omnivore, and pelagic feeder) is not random and the frequency at which these transitions occurred is relatively unbalanced (Gajdzik et al. 2019; McCord et al. 2021). Analyses of the evolution of the three ecotypes revealed that direct transition between the “specialist” benthic and pelagic feeders does not happen when the frequency of intermediate omnivore transitioning to the two “specialist” ecotypes is high. Accordingly, Gajdzik et al. (2019) suggested that the intermediate trophic guild may operate as a stepping-stone state towards specialized strategies in damselfishes.

Globally, the tempo of lineage diversification for the Pomacentridae is quite constant through time (Frédérich et al. 2013). However, recent works revealed that diversification rates are dependent on fish body size and trophic ecology (Gajdzik et al. 2019; McCord et al. 2021). Speciation rates were the highest among medium-sized damselfishes in comparison with small and large species (McCord et al. 2021). Concerning variation in diversification rates among ecotypes, the results from Gajdzik et al. (2019) and McCord et al. (2021) slightly differ but the differences could certainly be explained by the taxon sampling in phylogenies and the used comparative analyses. Both studies estimated that the benthic feeders are characterized by the lowest rate of diversification in comparison with the pelagic planktivores and the intermediate omnivores.

Recent advances in damselfish phylogenetics with large taxon sampling and associated chronograms provide the tools to study the successful radiation of Pomacentridae in coral and rocky reef environments. Additional works are certainly still needed to decipher all the factors explaining their success, even if their morphology and their versatility are probably key components allowing the observed easy shifts among a limited set of trophic ecotypes. By developing their symbiotic relationships with giant sea anemones, clownfishes represent a peculiar tribe within Pomacentridae. Our understanding of clownfish evolution characterized by their singular adaptations is challenging and the progress of clownfish research must pass through the identification

of their sister lineage within Pomacentrinae. Unfortunately, recent exhaustive phylogenies are not yet congruent about sister groups of clownfishes but the best candidates are certainly the genera *Pomacentrus*, *Neopomacentrus*, and *Amblypomacentrus*.

ACKNOWLEDGEMENTS

I gratefully acknowledge the editor, Vincent Laudet, Mark Westneat and one anonymous reviewer for their insightful comments and helpful criticism of the original manuscript. I thank M. Erdmann and F. Charpin, who kindly shared their photos of damselfishes allowing the making of Figure 1.1.

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