Biology of Butterflyfishes

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Foreword

The chaetodontids, popularly known as butterflyfishes, are a group that to both the public and the scientific community are highly representative of coral reef ecosystems. This reflects not only the diversity of highly visible and strikingly coloured species but their strong association with living corals both as a source of nutrition and as a habitat for newly recruited individuals. Indeed a number of earlier publications visualised this not as a passive linkage but as a functionally important association that provided an insight into the prevailing and future health of coral reefs. The role of chaetodontids as "indicator" species in the context of reef health ensured this group maintained a high profile in the coral reef literature and focused attention on obligate associations with living corals and trends in abundance linked to disturbances in reef ecosystems. However recent research has identified demographic and physiological properties of corals that provide direct metrics of their health and fitness, but more importantly have revealed a high diversity of behavioural, ecological and evolutionary processes in the chaetodontids themselves. The latter findings have enhanced our understanding of this group not just as obligate corallivores tied closely to living corals, but as a speciose group of perciforms with a complex biogeography and evolutionary history, a wealth of behavioural and life history features and a diversity of feeding interactions with the reef biota. In this context chaetodontids represent an ecological and evolutionary prism that allow us to probe the historical nature of associations of reef fishes with the changing profiles of Cenozoic reefs, the circumstances under which species may limit or expand consumption of food resources and the patterns of response to disturbance at both ecological and evolutionary time scales. And although the now-clarified fossil record of this group is sparse, the increasing focus on phylogenetic reconstruction and phylogeography has provided a platform for rigorous biogeograpical analysis, investigation of patterns in the evolution of trophic and behavioural traits and geographical vs. ecological processes of speciation.

The significance of chaetodontids and especially the genus *Chaetodon* in the context of ecological and evolutionary studies can be summarized by three observations; i) They occur within a range of reef ecosystems manifesting very different geological histories and prevailing oceanographic conditions; ii) They show a pattern of feeding behaviour that provides an unparalleled opportunity to identify food resources, establish the degree of trophic specialization and show how nutritional and foraging profiles vary with temporal and spatial change; iii) Their distinctive colour patterns and behaviours allow close and detailed observation of reproductive and feeding patterns in undisturbed groups. Dietary patterns and foraging especially in the genus *Chaetodon,* have provided a critical focus in evaluating how both evolutionary history and current ecological circumstances have shaped these traits. The fact that members of this genus occur in all of the world's great tropical ocean basins, each with a unique history and prevailing oceanographic conditions, provides a key to evaluating the hierarchy of events from evolutionary to ecological that have shaped feeding behaviours. The large number of species (many endemic) that occur in regions with turbulent oceanographic histories or currently marginal conditions is especially useful in this context. The endemic species of the Red Sea and Persian Gulf, reef systems that are subject to highly variable conditions over evolutionary and ecological time scales, provide a counterpoint for comparative studies over the broader Indo-Pacific. However although the taxonomic structure of chaetodontids is better known than many other groups of reef fishes for individual species, the match between genetic structure and phenotypes, and the propensity to hybridise in specific locations, reminds us that reconstructing patterns of species divergence will be a challenge.

An intriguing aspect of current studies concerns the history and biogeographic distribution of feeding specialisation, specifically the emergence and frequency of obligate feeding on hard corals. Although corals appear to represent an abundant food resource for benthic feeding reef fishes, it is noteworthy that relatively few species have evolved the capacity to use them. These species are dominated by members of the genus *Chaetodon*. Feeding limited to specific taxa of hard corals appears to be the ultimate in resource specialisation. However it is worth remembering that individual corals represent a diverse repository of food sources ranging from animal tissue, microscopic plant assemblages, mucous and tissues enriched to varying degrees by bacterial content. Although the external manifestations of feeding behaviour indicate a high level of specialisation it is unclear what components of the corals are targeted in a nutritional context, something that may vary between species and locations. Probing the nexus between feeding and nutritional targets in species which specialise on hard corals represents an area that will repay increased research investment.

One of the most important findings in an evolutionary context is the strong support for the hypothesis that critical episodes of chaetodontid diversification occurred during the Miocene, at a period when the distribution, structure and composition of coral reefs achieved a “modern” configuration. This pattern which seems such an obvious consequence of an integrated evolutionary development of corals and reef fishes urges a caveat. The temptation to develop one-size-fits-all approaches to the ecology and evolution of reef fishes should be tempered with detailed examination of other groups of reef fishes. The emerging picture suggests unique clade and taxon-specific histories in reef fishes in the context of the geological evolution of Cenozoic reefs and their associated oceanographic conditions. There is a need to identify those episodes in the evolution of reef fishes that can be legitimately generalised to a wide range of taxa. The most appropriate pathway for accomplishing this is to provide integrated perspectives on the evolutionary history and ecology of critical groups of reef fishes, perspectives that allow rigorous comparisons between major clades. The group of studies encapsulated in this volume represent a major advance in achieving this goal.

John H. Choat

Contents

CHAPTER 1

The Origins and Diversification of Coral Reef Butterflyfishes

David R. Bellwood[1,*] and *Morgan S. Pratchett*[2]

INTRODUCTION

The Chaetodontidae is a diverse family of percomorph fishes represented by 122 extant species, characterised by deep compressed bodies, small protruded mouths and bristle-like teeth (Allen et al., 1998). The family is dominated by fishes of the genus *Chaetodon*, which are among the most conspicuous inhabitants of coral reef environments. Two thirds of all butterflyfishes are found living within coral reef habitats, and many of these species feed mainly, if not exclusively, on reef-building corals (Cole et al., 2008; Cole and Pratchett, Chapter 5). Because of their reliance on corals for food, *Chaetodon* butterflyfishes are regarded among the most specialised and highly evolved coral reef fishes (e.g., Gosline, 1985). These fishes are inextricably linked to the corals on which they feed (Reese, 1977, 1981), but did the family originate within coral reef environments?

Reefs as we know them today are essentially a feature of the last 65 million years. The K/T (Cretaceous/Tertiary) boundary at 65 million years ago (Ma) marked the end of the Mesozoic era. In the seas, this was

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characterised by the loss of the ammonites and the end of the period in which rudist bivalves were the most significant feature of carbonate reefs (Wood, 1998). Thereafter, scleractinian corals became the dominant feature of carbonate reefs and these corals formed a distinctive component of carbonate reefs for the next 65 million years. However, it appears that scleractinian-dominated coral reefs and modern coral reef fish families first appeared and then diversified at approximately the same time, in the early Cenozoic (Bellwood, 1996; Bellwood and Wainwright, 2002; Wallace and Rosen, 2006). This suggests that the origins of modern coral reefs and their associated fish families are closely linked, and it is within this system that butterflyfishes (family Chaetodontidae) have proliferated, if not originated.

A fundamental step in understanding the origins of the family Chaetodontidae, is to establish the timing of their evolution relative to key points in the evolution of coral reefs. However, dating the earliest origins of the butterflyfishes, like any group of fishes, is difficult. There are basically two types of evidence that may be used: i) establishing the maximum age of fossils that unequivocally belong to the family Chaetodontidae, and ii) reconstruction of phylogenetic lineages based on either be morphological or molecular relationships, with dating calibrated using either biogeographic events, fossils or an inferred molecular clock. Each of these approaches has its advantages and limitations, but taken in concert, should provide a reasonably robust picture of the evolutionary history of the family. The two approaches are reciprocally illuminating but for ease of discussion each will be examined in turn.

RECORDS IN ROCK: DATING THE ORIGINS OF BUTTERFLYFISHES

For most coral reef fishes, the Eocene fossils from Monte Bolca in northern Italy mark the earliest record, dated to approximately 50 million years old. The fossils of Monte Bolca were laid down in deep waters in the vicinity of shallow tropical coastal ecosystems which contained both sea grasses and hard substrata, probably including some coral outcrops. These deposits mark the first documented record of numerous reef fish families such as the Acanthuridae, Labridae, Pomacentridae, Ephippidae and many others (Bellwood, 1996). For many years this also included the Chaetodontidae. Numerous Monte Bolca specimens were originally identified as belonging to the family Chaetodontidae. Most species are in the genus *Pygaeus* (8 species) (Fig. 1.1) but other chaetodontid genera include *Parapygaeus*, *Malacopygaeus* and *Acanthopygaeus* (Blot, 1980; Bannikov, 2004). In addition, Frickhinger (1991) inadvertently illustrated the Bolca enoplosid *Enoplosus pygopterus* as *Pygaeus gazolai* and placed it within Chaetodontidae.

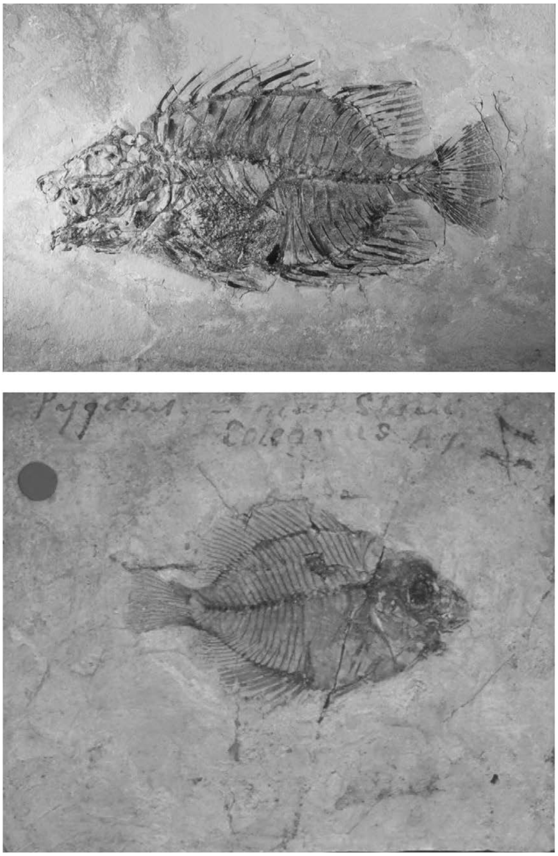

Fig. 1.1 For many years the earliest fossil record of the Chaetodontidae was associated with a number of *Pygaeus* species from the Eocene deposits of Monte Bolca in northern Italy. Many, like *Pygaeus agassizi* Eastman (top panel) were relatively large predatory forms, others like *Pygaeus coleanus* Agassiz (bottom panel) were smaller but with no morphological links to the family (Bannikov, 2004). *P. coleanus* is now regarded as a generalized percoid in the *incertae sedis* genus *Blotichthys*.

Unfortunately, none of these Bolca specimens were identified based on synapomorphies (derived anatomical features) that are characteristic of the family Chaetodontidae, which is a critical step in the accurate placement of species within higher taxonomic groupings. As with the Pomacentridae (Bellwood and Sorbini, 1996), parrotfishes (formerly Scaridae) (Bellwood and Schultz, 1991) and others (Blot, 1980), the earliest records attributed to the family Chaetodontidae were erroneous. In a recent re-evaluation, Bannikov (2004) rejected all Eocene material previously placed within the family. One is probably best placed in the Enoplosidae, the remainder remain *incertae sedis* (of uncertain affinity).

The recently described *Frigoichthys margaritae* has some chaetodontid affinities but in many ways it more closely resembles extant species in the family Microcanthidae. Microcanthids have broad superficial similarity to the Chaetodontidae (which is why they are included in the modern identification books as relatives (cf. Kuiter, 2002)), although microcanthids probably have greater affinity with the Kyphosidae than the Chaetodontidae (Smith and Wheeler, 2006). Several other Bolca specimens have chaetodontid-like characteristics (e.g., *A. gazolai*), but none are clearly placed within the family or can be readily identified as immediate sister taxa.

Discounting the Monte Bolca material, the earliest recorded fossil from the family Chaetodontidae is *Chaetodon penniger* (Bogachev, 1964) from the Rupelian (29–35 Ma) of Transcaucasia. This specimen is accepted by both Patterson (1993) and Bannikov (2004) as a chaetodontid. However, the basis for this decision is not clear and its status does not appear to have been critically examined in a phylogenetic context. Its status therefore, remains equivocal. A somewhat later specimen, *Chaetodon fisheuri,* was described from the Miocene of Algeria, in northern Africa. Originally described in 1927 by Arambourg, it has recently been re-examined (Carnevale, 2006) and can be placed with some confidence within the family. This fully articulated specimen bears a strong resemblance to extant butterflyfishes (Fig. 1.2).

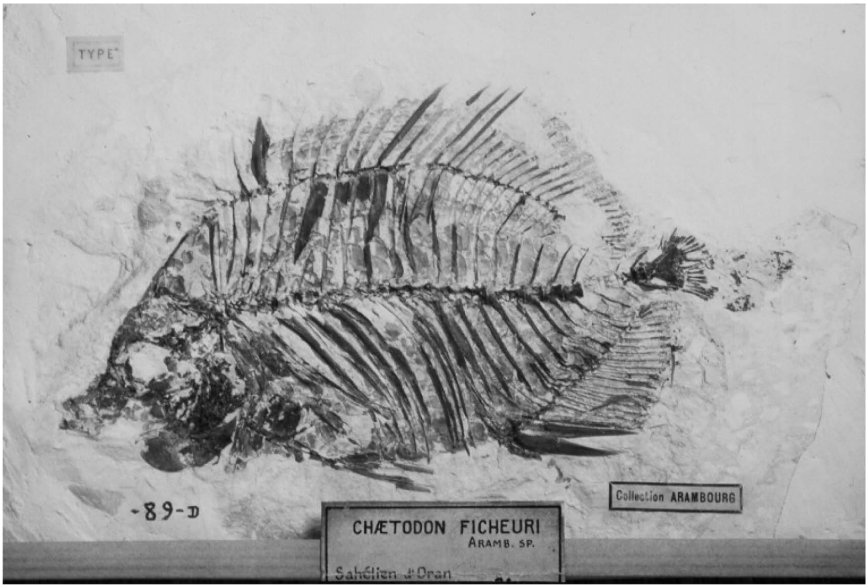

Fig. 1.2 *Chaetodon ficheuri* Arambourg from the deposits of Oran in northern Algeria is of late Miocene age. Exceptionally well preserved and clearly belonging to the family, this species has recently been re-examined (Carnevale, 2006).

Based on the fossil record, therefore, we can confidently say that the Chaetodontidae were present in the central-western Tethys, in the region now occupied by the Mediterranean, in the Miocene (5–25 Ma). There is also a strong possibility that butterflyfishes were present in the waters covering Western Europe during the Oligocene (29–35 Ma).

Phylogenetic Evidence

Robust phylogenies convey information on relationships and the relative ages of taxa. With appropriate calibrations, phylogenies can also yield valuable information on the likely ages of major lineages and the evolution of key character traits (e.g., Bellwood, 1994; Bellwood et al., 2004; Cowman and Bellwood, 2011). In recent years, the development of phylogenies based on molecular data has profoundly changed our view of chaetodontids and their relationships, and opened a new chapter in our understanding of the evolution of the group.

The Chaetodontidae were for a long time grouped with other fish families that share a similar body morphology. These deep bodied fishes were collectively termed the higher Squamipinnes (a group characterised by lateral compression and having scales (*squami*) on the bases of the fins (*pinnes*)). The higher Squamipinnes tentatively included the Ephippidae, Drepanidae, Scatophagidae, Pomacanthidae, Chaetodontidae, and the Acanthuroidei, namely the Zanclidae, Luvaridae, Siganidae and Acanthuridae (Tyler et al., 1989). However, this grouping (i.e., the monophyly of the higher squamipinnes) has been questioned and it almost certainly represents a polyphyletic group (Near et al., 2012).

Evolutionary relationships among the families formally ascribed to the higher Squamipinnes are yet to be fully resolved, with several recent analyses producing different topologies (e.g., Smith and Wheeler, 2006; Yagishita et al., 2009; Near et al., 2012). What is clear, however, is that the traditional relationship between butterflyfishes (Chaetodontidae) and angelfishes (Pomacanthidae) is well supported by molecular data (Bellwood et al., 2004; Smith and Wheeler, 2006; Yagishita et al., 2009). This suggests that numerous shared attributes between these families, including body shape, colour patterns, larval morphology, and tooth morphology, have a common evolutionary basis.

Based on a chronogram, constructed using Bayesian inference with multiple parametric priors, Bellwood et al. (2010), and later Cowman and Bellwood (2011), estimated that the family Chaetodontidae originated in the early Eocene (41.5–60.7 Ma) when it split from the Pomacanthidae. Ancestral range reconstructions suggesting that the origins and earliest diversification of the family were in the vicinity of the Indo-Australian Archipelago (Cowman and Bellwood, 2013).

Intra-relationships within the Chaetodontidae

There have been a number of phylogenies constructed for the family Chaetodontidae. The first cladogram, using morphological features, was constructed by Blum (1989) and expanded by Smith et al. (2003). These phylogenies were quickly followed by analyses using molecular data (e.g., Fessler and Westneat, 2007; Bellwood et al., 2010). The early morphological and later molecular phylogenies, however, produced discordant topologies. Although the morphological and molecular phylogenies agree in many respects, they differed in the placement of key taxa, especially *Amphichaetodon* (cf. Smith et al., 2003; Bellwood et al., 2010). In recent years, two large molecular phylogenies of the family have been produced (Fessler and Westneat, 2007; Bellwood et al., 2009). They used different representative taxa from each genus or subgenus and different molecular markers (although both included nuclear and mitochondrial DNA). The resultant phylogenetic trees were almost identical, giving considerable confidence in the inferred relationships and topologies of the trees (the two trees were subsequently combined by Cowman and Bellwood, 2011). It is these trees that will be used to explore intra-relationships with the family Chaetodontidae.

The taxonomy of generic and subgeneric groups within the Chaetodontidae is confusing. As extremely colourful fishes, they have attracted a lot of attention (Allen et al., 1998; Kuiter, 2002). This, along with a limited range of character states, has led to a multitude of generic and subgeneric names. The Chaetodontidae contains two distinct clades: the bannerfishes and the butterflyfishes (Fig. 1.3). The bannerfishes are the smaller of the two clades with just 25 species. Although small, this is a morphologically diverse clade with eight distinct genera. All eight existing genera are strongly supported by the molecular phylogenies (Fessler and Westneat, 2007; Bellwood et al., 2010; Cowman and Bellwood, 2011). These genera are not very species rich but the generic divisions are stable and distinct. The butterflyfishes, in marked contrast, are problematical.

The other major division of the family Chaetodontidae, the butterflyfishes, have just two genera but contain at least 103 species (Table 1.1). Numerous species, a lack of reliable morphological characters, and a series of revisions have resulted in a plethora of generic or subgeneric groupings. This taxonomic confusion is discussed in detail by Fessler and Westneat (2007). Basically, there is a great deal of inconsistency and the existing taxonomic classification is of little ecological, evolutionary or systematic utility. Only two genera are supported by the latest molecular phylogenies, *Prognathodes* (10 spp.) and its sister taxon *Chaetodon* (93 spp.; including the monotypic *Parachaetodon*). There are four well supported subgeneric clades within the genus *Chaetodon*, but these do not agree with any existing subgeneric

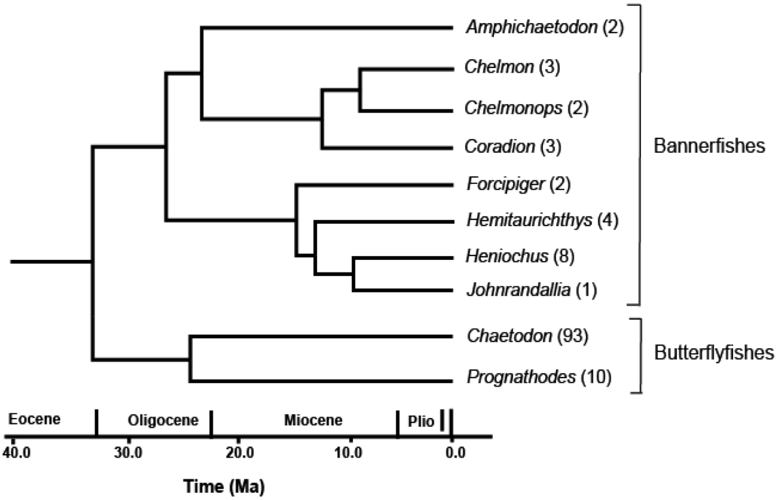

Fig. 1.3 A phylogeny of genera within the Chaetodontidae (modified after Bellwood et al., 2010). The number of species is given in parentheses.

classifications (e.g., *Megaprotodon*; taxonomic details are given in Fessler and Westneat, 2007). Fessler and Westneat (2007), Bellwood et al. (2010) and Cowman and Bellwood (2011) refer to these clades by number, 1 to 4. These clades are of considerable ecological utility; indeed the phylogenetic structure of the family underpins significant ecological and evolutionary divisions in terms of morphological innovation, biogeographic history, habitat associations, the evolution of trophic modes and susceptibility to climate change (Bellwood et al., 2010).

The bannerfishes and butterflyfishes are of comparable age (as sister taxa) but differ markedly in species numbers. This may in part reflect their biogeographic history and patterns of habitat association. The bannerfishes initially diverged from the butterflyfishes at about 26.1 Ma with divisions of the remaining bannerfish lineages between 8 and 23 Ma: *Amphichaetodon* (22.9 Ma), *Coradion* (11.9 Ma), *Chelmonops* and *Chelmon* (8.4 Ma). The bannerfish clade reflects similar patterns of Miocene diversification, at a generic level, as seen in other reef fish families such as the Labridae and Pomacanthidae (e.g., Bellwood et al., 2004; Bernardi et al., 2004; Barber and Bellwood, 2005; Cowman et al., 2009). Likewise, separation of the two *Chelmonops* species at 0.9 Ma (*curiosus* in West Australia; *truncatus* in East Australia) and possible parapatric speciation in the three species in the *Chelmon rostratus* lineage at 3.8 (*C. muelleri*—NE Australia) and 1.5 Ma (*C. marginalis*—NW Australia) reflect Pliocene division and origination of species as seen in other reef fish families (cf. Fauvelot et al., 2003; Bernardi et al., 2004). In the bannerfishes these species divisions appear to be associated with Pliocene vicariance around the Australian continent.

Table 1.1 A species list of bannerfishes and butterflyfishes. Generic and clade affiliation, diet and habitat follow Bellwood et al. (2010). Corallivores were defined as those species with more than 80% of corals comprising the diet. Reef habitat codes: coral (C), rocky (R), deep (D), sedimentary (S), rubble (RU), oceanic (O), algal (A), coastal (CO), coastal weedy (CW), inshore (I). **Note there are at least 4 more species to be named (Allen et al., 1998; Kuiter 2002).

Major clades	**Genus/ minor clade**	**Species**	**Diet**	**Habitat**
Bannerfishes	*Amphichaetodon*	*howensis*	?	R
		melbae	?	R
	Chelmon	*marginalis*	Omnivore	CO, S
		muelleri	Omnivore	CO, S, A
		rostratus	Omnivore	D, CO, S
	Chelmonops	*curiosus*	Omnivore	R
		truncatus	Omnivore	D, R
	Coradion	*altivelis*	Omnivore	C, S
		chrysozonus	Omnivore	R
		melanopus	Omnivore	D, C
	Forcipiger	*flavissimus*	Omnivore	C
		longirostris	Omnivore	C
	Hemitaurichthys	*multispinosus*	Omnivore	D
		polylepis	Omnivore	C
		thompsoni	Omnivore	D
		zoster	Omnivore	C
	Heniochus	*acuminatus*	Omnivore	CO, D
		chrysostomus	Omnivore	C
		diphreutes	Omnivore	D
		intermedius	Omnivore	C
		monoceros	Omnivore	C
		pleurotaenia	Omnivore	C
		singularis	Corallivore	D, CO
		varius	Omnivore	C
	Johnrandallia	*nigrirostris*	Omnivore	C, R
Butterflyfishes	*Chaetodon* (Clade 1)	*hoeferi*	Omnivore	R, S
		robustus	Omnivore	R, C
		marleyi	Omnivore	R, C
	Chaetodon (Clade 2)	*argentatus*	Omnivore	C, RU
		assarius	Omnivore	C
		blackburnii	Omnivore	R, C
		burgessi	Omnivore	D, C
		cintrinellus	Omnivore	R
		daedalma	Omnivore	R
		declivis	Omnivore	R, D
		dialeucos	Omnivore	

Table 1.1 contd....

Table 1.1 contd.

Major clades	**Genus/ minor clade**	**Species**	**Diet**	**Habitat**
		dolosus	Omnivore	D
		excelsa	?	D, R
		flavocoronatus	Omnivore	D
		fremblii	Omnivore	R, C
		guentheri	Omnivore	R, C
		guttatissimus	Omnivore	C, S
		guyotensis	Omnivore	
		interruptus	Omnivore	C
		jayakari	?	D, R
		kleinii	Omnivore	R, C
		interruptus	Corallivore	C
		litus	Omnivore	R, C, A
		madagaskariensis	Omnivore	C
		mertensii	Omnivore	R, C
		miliaris	Omnivore	C
		mitratus	Omnivore	C
		modestus	?	R
		multicinctus	Corallivore	C
		nippon	Omnivore	R
		paucifasciatus	Omnivore	RU, C
		pelewensis	Omnivore	C
		punctatofasciatus	Omnivore	C
		quadrimaculatus	Corallivore	R, C
		sanctaehelenae	Omnivore	R
		sedentarius	Omnivore	C
		smithi	Omnivore	R
		tinkeri	Omnivore	C, D
		trichrous	Omnivore	C
		unimaculatus	Corallivore (soft)	C
		xanthurus	Omnivore	C
	Chaetodon (Clade 3)	*andamanensis*	Corallivore	C
		aureofasciatus	Corallivore	C, A
		austriacus	Corallivore	C
		baronessa	Corallivore	C
		bennetti	Corallivore	C
		larvatus	Corallivore	C
		lunulatus	Corallivore	C
		melapterus	Corallivore	C, S

Table 1.1 contd....

Table 1.1 contd.

Major clades	**Genus/ minor clade**	**Species**	**Diet**	**Habitat**
		meyeri	Corallivore	C
		octofasciatus	Corallivore	C, S
		ornatissimus	Corallivore	C
		plebius	Corallivore	C
		rainfordi	Corallivore	C
		reticulatus	Corallivore	C
		speculum	Corallivore	C
		triangulum	Corallivore	C
		tricinctus	Omnivore	C
		trifascialis	Corallivore	C
		trifasciatus	Corallivore	C
		zanzibariensis	Corallivore	C
	Chaetodon (Clade 4)	*adiergastos*	Omnivore	C
		auriga	Omnivore	C
		auripes	Omnivore	R, C, CW
		capistratus	Omnivore	C
		collare	Omnivore	C
		decussatus	Omnivore	R, C
		ephippium	Omnivore	C
		falcula	Omnivore	C
		fasciatus	Omnivore	C
		flavirostris	Omnivore	C, R
		gardineri	Omnivore	CO
		humeralis	Omnivore	R
		leucopleura	Omnivore	C, S, RU
		lineolatus	Omnivore	D, C
		lunula	Omnivore	R, C
		melannotus	Corallivore (soft)	C
		mesoleucos	Omnivore	C
		nigropunctus	Omnivore	R, C
		ocellatus	Omnivore	C
		ocellicaudus	Corallivore (soft)	C
		oxycephalus	Omnivore	C
		pictus	Omnivore	
		rafflesi	Omnivore	C
		selene	Omnivore	S, C
		semeion	Omnivore	C

Table 1.1 contd....

Table 1.1 contd.

Major clades	Genus/ minor clade	Species	Diet	Habitat
		semilarvatus	Omnivore	C
		striatus	Omnivore	R, C
		ulietensis	Omnivore	C
		vagabundus	Omnivore	C
		wiebeli	Omnivore	R, C
		xanthocephalus	Omnivore	C, I
	Prognathodes	*aculeatus*	Omnivore	C, D
		aya	Omnivore	D
		brasiliensis	Omnivore	R
		dichrous	Omnivore	R
		falcifer	Omnivore	R, D
		guezei	Omnivore	D
		guyanensis	Omnivore	R, D
		guyotensis	?	O
		marcellae	Omnivore	D, R, C
		obliquus	Omnivore	R

This strong association between bannerfish and the Australian region is mirrored by a close association with temperate and rocky reef habitats. Among the bannerfishes, 3 out of 8 lineages are found on temperate subtropical rocky reefs and many species in the other lineages are found in rocky, deep, or coastal waters (Table 1.1). Moreover, it is noteworthy that there are no bannerfishes in the Atlantic, despite the presence of *Johnrandallia* in the East Pacific, which split from *Heniochus* at about 9.0 Ma (Bellwood et al., 2010). This early division suggests that the bannerfish clade may have been present in the Americas (East Pacific and tropical Atlantic) prior to the closure of the Isthmus of Panama. In this scenario, the absence of bannerfishes from the Caribbean today would be the result of regional extinction, as in the surgeonfish genus *Naso* (Bellwood and Wainwright, 2002). However, colonisation of the East Pacific by relatively old clades that arose in the Australian region of the West Pacific remains a distinct possibility (cf. Burridge and Smolenski, 2004).

Diverging from the *Chaetodon* lineage at about 23 Ma, *Prognathodes* closely resembles the bannerfishes, with a long snout and deep rocky reef associations. It also shares their limited diversity. *Prognathodes* is most speciose in the Atlantic with 6 of the 10 species. This genus is relatively large compared to the bannerfishes where *Heniochus* is the largest genus with just 8 species. However, it is in *Chaetodon* that we see the most spectacular diversification with 93 species. It is in this genus that we first see a distinct move onto coral reefs and where there is the most corallivory. Analyses of relative rates of diversification strongly suggest that it was the habitat shift onto coral reefs, and not a dietary shift to corallivory, that underpinned the significant diversification within the genus (Bellwood et al., 2010). This pattern appears to be a relatively widespread phenomenon, with a number of reef fish groups diversifying after moving onto reefs, including the Tetradontiformes, Labridae, Pomacentridae and Apogonidae (Alfaro et al., 2007; Bellwood and Wainwright, 2002; Cowman and Bellwood, 2011).

Phenotypic Diversity

In terms of morphological innovation, the most remarkable changes are seen within the bannerfishes. The bannerfishes exhibit several extreme morphologies. Some, such as the tubemouthed *Coradion,* are of unknown functional significance (although the similarity with tubemouthed labrids may suggest mucous feeding or corallivory), while others have been carefully examined. Foremost among these is the unique suspensorial rotation seen in *Forcipiger* and *Chelmon* (Ferry-Graham et al., 2001a, b). In these taxa the usually stationary suspensorium (the bones that support the mouth closing muscles in the 'cheek') is articulated enabling the fishes to project their jaws forward at high speed. In *Forcipiger longirostris* the suspensorial rotation enables to jaws to move forward more than twice as far as other chaetodontid species. This extreme protrusion of the jaws enables them to snatch small caridean shrimps from benthic substrata (Ferry-Graham et al., 2001a, b).

In contrast to the bannerfishes, the butterflyfishes are morphologically conservative; The major axis of variation being the extent of intermandibular rotation (Konow et al., 2008; Konow and Ferry-Graham, Chapter 2) and increasing jaw strength or gut length seen in certain coral feeding specialists (Elliott and Bellwood, 2003; Berumen et al., 2011). However, what they lack in phenotypic diversity they make up for in species diversity. Each of the four distinct clades with the genus *Chaetodon* has its own characteristic biogeographic and ecological features. *Chaetodon* Clade 1, the African butterflyfishes, contains just 3 species; all are restricted to coastal and marginal reefal systems on the west coast of Africa. *Chaetodon* Clade 2, containing omnivores, is pantropical with a wide diversity of species including several interesting and distinctive lineages. This includes: a) a deep dwelling lineage (*tinkeri* lineage), b) three separate corallivore lineages (*quadrimaculatus*, *multicinctus* and *unimaculatus*) that eat both soft and hard corals, and c) a relatively young Atlantic lineage (*sedentarius*, *sanctahelenae*). The age of this latter lineage at about 2 Ma and the location of the two component species suggest that this may be an example of colonisation of the Atlantic from the Indian Ocean via the Cape of Good Hope (cf. Bellwood et al., 2004; Cowman and Bellwood, 2012; reviewed by Floeter et al., 2008).

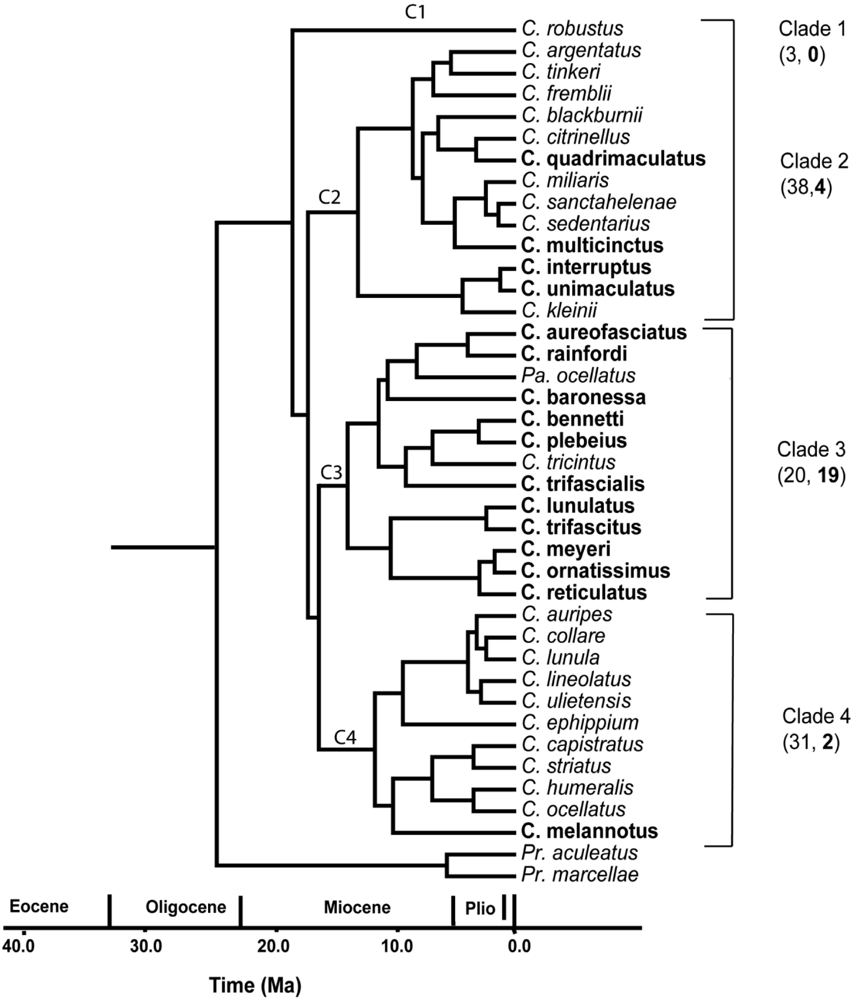

Fig. 1.4 Major clades within the genus *Chaetodon*. Species were selected to represent all traditional genera and subgenera (following Bellwood et al., 2010). The number of species in each clade and the number of obligate corallivores (in bold) is given in parentheses.

Chaetodon Clade 3, the coral feeders, is restricted to the Indo-Pacific. This is an unusual clade comprised almost entirely of obligate coral feeding species. This clade contains the most abundant and colourful butterflyfishes found on coral reefs. Within the group are almost all of the hard coral feeding specialists, including those which feed on just one or two coral species (Berumen and Pratchett, 2008), or that ingest specific parts of corals or just coral mucous (Cole et al., 2008). It is noteworthy that there is little evidence of any changes to the relatively generalised *Chaetodon* morphology in association with this switch to corallivory. Documented morphological changes are restricted to an increase in the length, and concomitant decrease in the diameter, of the intestine in some corallivorous species (Elliot and Bellwood, 2003) and slight modifications to the jaws. The largest degree of modification in the oral jaws, in terms of intramandibular flexion, is recorded in clade 3, in the subgenus *Citharoedus* (Konow et al., 2008, shown in the cladogram by the *C. meyeri-ornatissimus-reticulatus* clade. This appears to be an example of a specialised powerful biting coral feeding mode. Species within *Chaetodon* Clade 3 have the strongest links with coral reefs and it is these species that exhibit the greatest changes in response to the global decline in coral reef condition (Wilson et al., 2006; Pratchett et al., 2008).

Chaetodon Clade 4 contains mainly omnivores. It shares many similarities with clade 2. It has a circum-tropical distribution and contains numerous omnivorous species. There is only one corallivorous lineage (*C. melannotus-ocellicaudus*), but interestingly this is restricted to feeding on soft corals. As in the rest of the butterflyfishes all lines of evidence suggest that the main constraint on dietary changes is at the physiological level. This predation of soft corals appears to require specific biochemical adaptations to cope with secondary metabolites (Wylie and Paul, 1989; Coll et al., 1989). The sister lineage to the *melannotus* lineage contains almost all of the Atlantic chaetodontid species (there are no Atlantic bannerfishes).The remaining species in clade 4 are all restricted to the Indo-Pacific and are characterised by generalised dietary and habitat requirements.

Clade 4 contains the majority of Atlantic chaetodontid species. Like all other species in this clade, they are found on coral reefs, but many extend into non-reef habitats, including rocky reefs and coastal systems. The tropical Atlantic supports fewer chaetodontid species than the Indo-Pacific and contains no corallivores; it is the coral specialising clade 3 that is missing in the Atlantic. This absence of corallivores is consistent with the suggestion that reefs in the region support a more temperate fauna and that modern coral reef fish faunas in the Atlantic have a significant non-reefal composition (Bellwood and Wainwright, 2002). This may reflect repeated colonisation by taxa that refuge in or colonised from non-reef habitats (Bellwood, 1997; Floeter et al., 2008). In this regard, it is noteworthy that every Atlantic chaetodontid has been reported from non-reef habitats, and that the most diverse Atlantic chaetodontid genus (*Prognathodes*) is most frequently reported from deep rocky slopes and is rarely found on shallow coral reefs.

CONCLUSIONS

The evolutionary history of the family Chaetodontidae is a long one with close ties to coral reefs. Separating from their most recent common ancestor with the angelfishes about 50 Ma, the chaetodontids saw an early division into two groups (bannerfishes and butterflyfishes) at about 33 Ma (Bellwood et al., 2010). At this time the biodiversity hot spot for tropical marine taxa was in the European-Arabian region of the globe and it is from here that we find the earliest chaetodontid fossils. Shortly after this time we saw a move onto coral reefs (at about 18 Ma) which underpinned a significant increase in the diversity of the group. In the Atlantic however, these reefal links were limited or lost, and today they remain relatively weak. It was in the Indo-Pacific that the close relationship between coral reefs and chaetodontids (butterflyfishes in particular), proliferated. This close association is reflected by at least five separate occurrences of corallivory, starting at about 15.7 Ma in clade 3, with the youngest origination in the C. *quadricmaculatius* lineage in clade 2 at about 3.2 Ma (Bellwood et al., 2010). This increasing interdependency between the reef and its associated fishes coincides with the Miocene relocation of the world's largest marine biodiversity hotspot to the Indo Australian Archipelago (Bellwood et al., 2005; Renema et al., 2008). This location appears to have been the focus for the concatenation and development of modern coral reef faunas and, more importantly, the establishment of modern coral reef ecosystem processes (Cowman et al., 2009; Bellwood et al., 2010; Cowman and Bellwood, 2011, 2013).

The Miocene expansion of coral reef specialists fits in with escalating patterns of marine predation, but may mark a distinct third phase. Initially, the marine Mesozoic revolution was characterised by increased predation with resultant infaunalisation and armouring of prey (Vermeij, 1977). Following the K/T boundary, coral reefs experienced a Cenozoic grazing revolution, with the appearance of numerous groups of piscine herbivores (Bellwood, 2003). Finally, in the Miocene we see the rise of 'precision predation' with specialised taxa feeding on small flesh fragments, mucous or particulate material (Cowman et al., 2009; Bellwood et al., 2010). In this latter phase, butterflyfishes stand as one of the best examples of this novel expression of precision predation. Coral reefs and their associated fishes have shared a long history (Bellwood and Wainwright, 2002). However, few families have forged such a strong interdependency as the chaetodontids. The chaetodontids and most especially the butterflyfishes of clade 3 stand as the epitome of coral reef fishes.

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CHAPTER 2

Functional Morphology of Butterflyfishes

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INTRODUCTION

Butterflyfishes (family Chaetodontidae) have historically been grouped with several deep-bodied reef fish families into the squamipinnes, or *'scaly-finned'* fishes (Mok and Shen, 1982; Gosline, 1985; Blum, 1988; Tyler et al., 1989). However, it is presently uncertain whether this grouping is monophyletic (Konow et al., 2008). Apart from butterflyfishes (128 species worldwide; Fig. 2.1), and their purported sister-family (Burgess, 1974), the angelfishes, family Pomacanthidae (86 species), the squamipinnes are comprised of acanthuroid surgeonfishes (Acanthuridae), rabbitfishes (Siganidae) and the Moorish Idol (Zanclidae), the Kyphosidae (incl. microcanthids and girellids) and the fairly species-depauperate Ephippidae, Drepanidae and Scatophagidae (Tyler et al., 1989; Froese and Pauly, 2012).

Butterflyfish morphology has, in the past decades, primarily been investigated for the purpose of systematic classification (Mok and Shen, 1982; Smith et al., 2003; Blum, 1988) (Fig. 2.1). Until very recently (Littlewood et al., 2004; Hsu et al., 2007; Fessler and Westneat, 2007), phylogenetic

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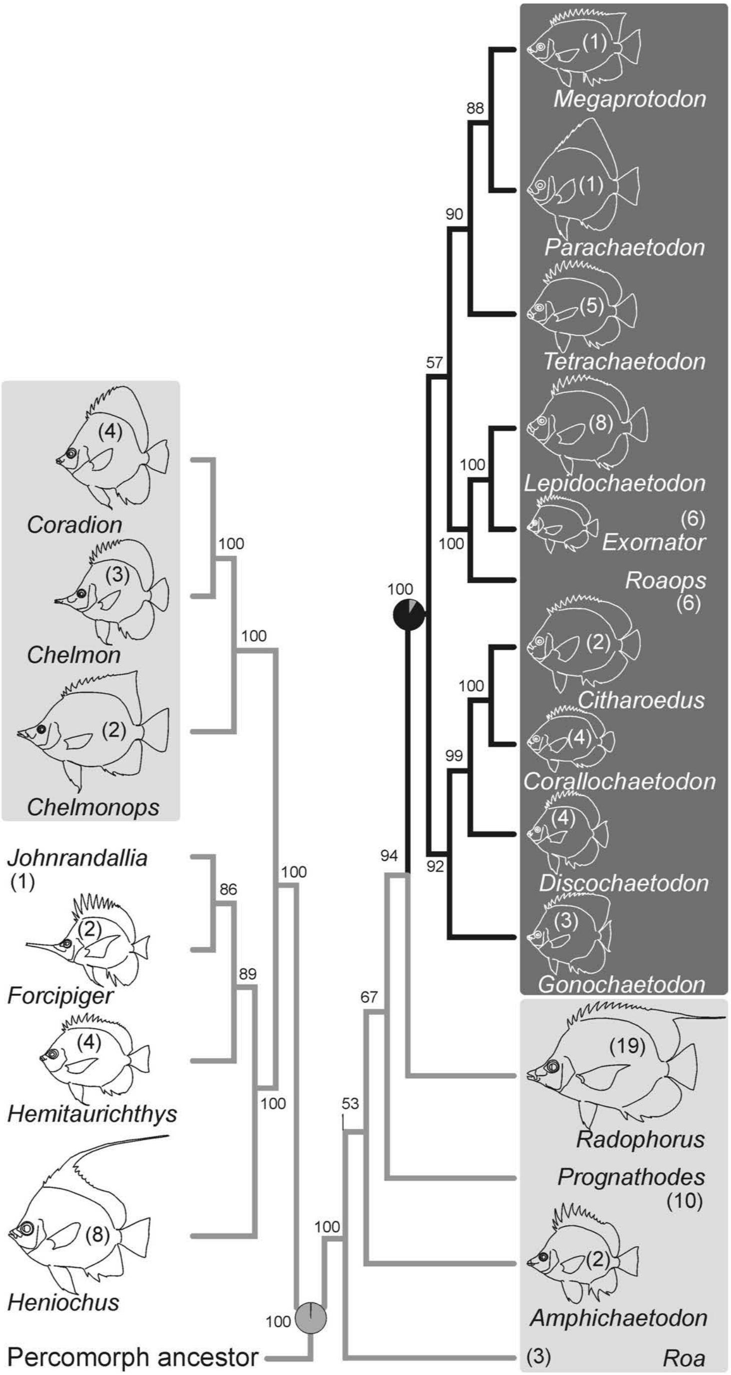
(1)
Megaprotodon
88
(1)
Parachaetodon
90
(5)
Tetrachaetodon
57
(8)
Lepidochaetodon
100
(6)
Exornator
100
Roaops
(6)
100
(2)
Citharoedus
100
(4)
Corallochaetodon
99
(4)
Discochaetodon
92
(3)
Gonochaetodon
94
(4)
Coradion
(3)
Chelmon
100
100
(2)
Chelmonops
Johnrandallia
(1)
86
(2)
Forcipiger
89
(4)
Hemitaurichthys
100
100
(8)
Heniochus
67
(19)
Radophorus
53
Prognathodes
(10)
100
(2)
Amphichaetodon
100
Percomorph ancestor
(3)
Roa

research on the family based on molecular data also lagged behind most of the other squamipinnes families (c.f. Tang et al., 1999; Clements et al., 2003; Bellwood et al., 2004). The lack of information on evolutionary morphology is puzzling, considering that this family has attained iconic status as coral reef fishes and marine ornamentals. This status has been assigned primarily based upon the key role of butterflyfishes as predators on stony (scleractinian) corals. While ecological studies of this derived feeding guild exist (for example Irons, 1989; Tricas, 1989; Alwany et al., 2003; Pratchett, 2005; Berumen and Pratchett, 2007), these tended to focus on regional patterns, and only very recently attempted to understand how butterflyfish accomplish their evolutionarily novel foraging tasks (Motta, 1985, 1989; Ferry-Graham et al., 2001a, b; Konow et al., 2008). Currently, the information relating morphology to ecology concerns a highly specialised pelagic *tholichthyes* larval morphology, the derived laterophysic canal structures involved in balance-maintenance and sound production (i.e., a joint locomotor and behavioural specialisation), the functional morphology of the locomotor apparatus itself, and a range of feeding specialisations based on novel origins of joints within the feeding apparatus.

Fig. 2.1 Interrelationships of the Chaetodontidae, reconstructed using data from Blum (1988), Ferry-Graham et al. (2001b), and Smith et al. (2003), which was modified using the super-tree technique Matrix-recombination with Parsimony (MRP). Fish icons are scaled to the mean of reported maximum body-sizes for those particular subgenera, the species number of which is given in brackets on the fish body. Branch-lengths are chosen for clarity of presentation only and numbers at branch nodes are bootstrap-values from the MRP analysis. Note how butterflyfishes naturally divide into two groups of banner and forceps fishes (left), and butterflyfishes (right). The following ecomechanic traits were mapped and optimised onto the tree in the Mesquite phylogenetics package module under maximum parsimony: Character-states for intramandibular joint (IMJ) possession are optimised to branches using black for presence and grey for absence of the joint. For the IMJ, the likelihood of the ancestral state (presumably the lack of an IMJ) was reconstructed as posterior probabilities and is reported using pie-charts at relevant nodes leading to the cladogenesis of the genus *Chaetodon.* Pie-chart shading corresponds with the branch optimising colour-scheme, and the second most probable state is indicated when its probability is greater than 0.05. Feeding mode is mapped onto the major clades using shaded boxes to delineate obligate and facultative coral-biting taxa (dark grey), those utilising both invertebrate-picking and ram-suction feeding guilds (light grey) and pure ram-suction feeders (white). Note that the combination of obligate biting strategies and possession of an IMJ coincides in the genus *Chaetodon* only. Moreover, butterflyfish jaw-lengths are typically intermediary to long in taxa that prioritise the ram-feeding end of the feeding mode continuum (see text). An exception to this rule is among members of the bannerfish clade (i.e., *Heniochus* and *Hemitaurichthys*), which commonly engage in suction-feeding planktivory. The biting *Chaetodon* butterflyfishes are, apart from their IMJ, characterised by having relatively short jaws that are mechanically efficient for biting. However, standing out are the forcepsfishes (*Chelmon* and *Chelmonops*) in their possession of ram-suction feeder traits (long jaws, suspensorial flexion; Fig. 2.4), while almost exclusively feeding using biting. For details on tree-construction, see Konow et al. (2008), from which this figure was modified with permission from the publisher.

Given the authors' expertise and the prevalent emphasis in the present volume on trophic ecology and dietary specialisations of these fishes, this chapter will treat the areas of hearing and sound production, locomotion, and feeding specialisations. In this chapter, we will take a functional morphological approach, specifically to summarise our present understanding of butterflyfish ecomechanics. We define ecomechanics as the link between organismal functional morphology (i.e., a biomechanical apparatus such as the fins or the jaws), and ecological performance, being the relative capacity and capability of the organism to use said apparatus to complete vital everyday tasks (in these cases, swimming and feeding).

Most of the recent studies of swimming and feeding have involved strong experimental components and have taken a comparative approach, and these studies can therefore be used to evaluate the relative advantage of certain structures over others in performing ecological tasks. Earlier swimming functional morphology studies (Webb, 1982; Gerstner, 1999a, b; Blake, 2004) proposed that species group into guilds depending on their swimming mode. More recently, Fulton (2007) measured the swimming performance of reef fishes empirically, in a flow tank, and conducted habitat-based validations of swimming performance. This approach served to identify characteristics of the fin apparatus that potentially explained prominent interspecific differences in swimming capability, which was then verified on the coral reef (Fulton, 2007). Similarly, in early analyses of feeding functional morphology, Motta (1982–1989) identified morphological characters within the feeding apparatus that differed across taxa and appeared to characterise different feeding guilds. Kinematics of the jaw apparatus were only measured more recently, using motion analyses of high speed video, which served to validate some functional hypotheses and refute others (Ferry-Graham et al., 2001a, b; Konow et al., 2008; but see pioneering attempts by Motta, 1985). Thus, while the earlier swimming and feeding work provided important morphological baseline knowledge, they were not really successful in terms of identifying links between morphology and ecology (i.e., eco-morphology; Motta, 1988; Wainwright, 1991). A major reason for this lack of early success could be that several salient ecomorphological relationships were only identified in later analyses, when a more integrative experimental approach could be incorporated.

Where comparative studies are lacking, we cannot place too much weight on inferred performance consequences. However, we can draw on extensive personal observations, including video documentation, from reefs and aquaria in order to make inference about organismal function. In the following, we are careful to place those inferences within an appropriate cautionary framework, adhering to the adage that one cannot infer function without directly measuring it (Motta, 1988; Wainwright, 1991).

THE MECHANOSENSORY SYSTEM

Butterflyfish have been well studied in the context of mating systems and the associated behavioural ecology of mating (e.g., Yabuta and Berumen, Chapter 8). Recently, we have begun to understand the unique functional morphological underpinnings of these behaviours. This work falls into two general areas: the study of chaetodontid hearing and the associated laterophysic canal system, and the concomitant study of chaetodontid sound production.

The Laterophysic System

The laterophysic system is unique to chaetodontids and involves a pair of projections, on the right and left sides of the body, extending from the swim bladder to the posterior region of the neurocranium. These projections create a connection with the lateral line canal located within the supracleithrum (Fig. 2.2A), although the specifics of the structure varies among species (Webb and Smith, 2000; Smith et al., 2003; Webb et al., 2006). This connection was named the laterophysic connection due to its morphological similarly to otophysic connections (Webb, 1998a; Webb and Smith, 2000); which are connections found in other fishes (i.e., otophysans) that have specialised hearing (reviewed in Webb et al., 2006).

It is hypothesised that the function of the laterophysic connection is to increase the sensitivity of the accoustico-lateralis system, the inner ear plus the lateral line, to sound pressures. Receiving sound is typically the role of the pars inferior, or the ventral portion of the inner ear. The inner ear is composed of three semi-circular canals projecting in the three dimensions. The ventral portions of the inner ear contain three chambers that each house a dense crystalline structure; these are collectively called otoliths. These otoliths rest on a bed of sensory hair cells that have an afferent connection directly to the nervous system. As a fish is nearly the same density as water, sound waves tend to pass through the fish. The dense otoliths, however, vibrate when sound waves impact them. These vibrations set the hair cells in motion and thus the sound information is transferred to the brain for processing. The lateral line also contains sensory hair cells, also referred to as lateral line neuromasts, which are similar in structure and function to the inner ear hair cells (although there are both afferent and efferent neuronal connections). The lateral line is typically used for receiving far field sound; low pressure waves that transmit at lower frequencies and over longer distances (Kalmijn, 1989).

The swim bladder contains air and is therefore also of a different density than the fish, and the surrounding medium. Therefore, it can also act as a receiver of sound waves being transmitted through the water. By extending

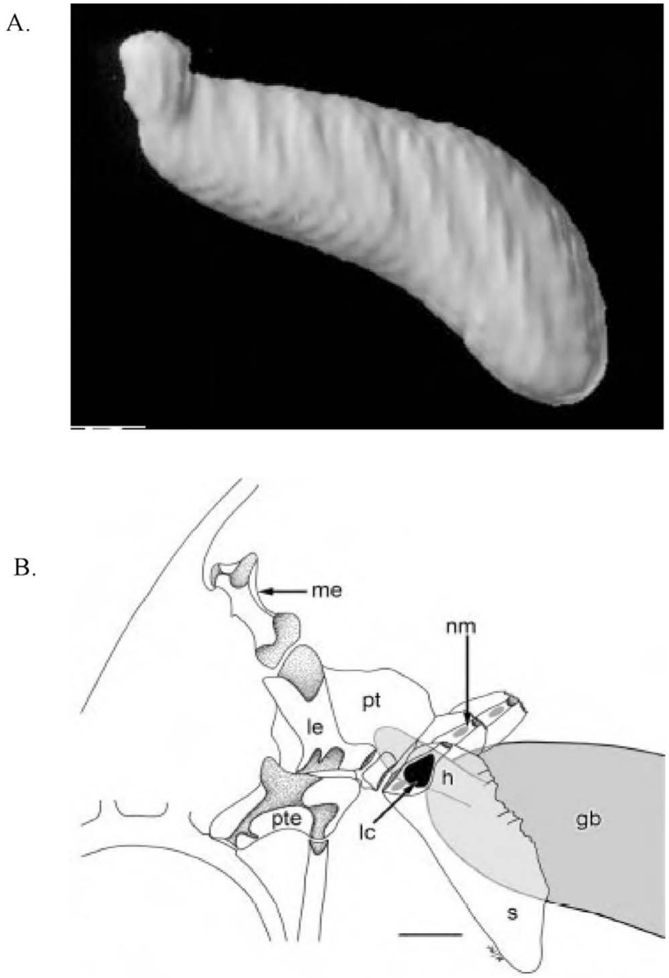

Fig. 2.2 3D CT reconstruction of the volume of the swim bladder and swim bladder horns in *Chaetodon punctofasciatus* **(A)** periodic indentations in lateral surface correspond to ribs, and **(B)** camera lucida drawing of skeletal elements posterior to the orbit at the posterior margin of the skull in *Chaetodon octofasciatus.* gb, swim bladder; h, horn; le, lateral extrascapular; me, medial extrascapular; nm, neuromast; pt, posttemporal; pte, pterotic; s, supracleithrum. Scale bars 1 mm. Modified after Webb et al. (2006) with permission from the publisher.

projections towards the sensory apparatus of the accoustico-lateralis system, the sound waves intercepted by the swim bladder are transmitted to the nervous system for processing (Schellart and Popper, 1992). Variants on the nature of the connection between the swim bladder horns and the lateral line in species of *Chaetodon* are thought to be directly related to the degree of enhancement of sound reception.

The variations range from a direct to an indirect connection between the projections of the swim bladder and the lateral line (Fig. 2.2B). A direct connection consists of layers of tissue that act as a tympanic membrane resting between the fluid filled lateral line and the air-filled swim bladder. Thus, sound waves received by the swim-bladder are putatively converted to fluid flow in the lateral line system, where they can be processed by the nervous system (Webb et al., 2006). This tympanum may be well developed, consisting of up to 4 layers of mucoid tissue, or less strongly developed and formed of only two layers of non-mucoid tissue. Generally, if the tympanic connection is less developed, the swim bladder is subdivided into two sections anteriorly and posteriorly. The projections of the swim bladder tend to be relatively long to facilitate this connection, though they vary in width. Indirect laterophysic connections contain a physical space between the swim bladder projections and the lateral line, ranging from 0.2 mm to 1 mm. Mucoid tissue may or may not be present, and the projections of the swim bladder may be long or short.

Sound Production

The presence of such elaborations for sound reception led researchers to speculate that sound production might also be present in *Chaetodon* species. Indeed, a single series of field experiments verified that sounds were produced in a variety of social contexts, including territorial displays and alert calls (Tricas et al., 2006), and this study is summarised here. Sounds were evoked by placing a single fish within the territory of a pair of *Chaetodon multicinctus.* This species is monogamous, has strong site fidelity, and is aggressive. It is also known that visual signals are fundamentally important in this species as a means of communication on the reef. From a functional morphological perspective, the production of these sounds is interesting because they assign a function to a particular mechanical movement.

The sounds recorded from this species can be grouped into motor-based and acoustic-based sounds (Tricas et al., 2006). Four motor-based sounds were recorded that were associated with actual movement of portions of the body; the tail-slap, the jump, the pelvic-fin flip, and the dorsal-anal fin erect (Fig. 2.3). Each of these movements, produced by resident fishes in this context, presumably sends a visual signal to conspecifics. However, the motion of the body also produced a recordable sound within the hearing range of chaetodontid fishes. These were low frequency, hydrodynamic sounds associated largely with the flow of water induced by the fin movement. The sounds were typically between 50 and 200 Hz peak frequency, and most lasted from 20–150 milliseconds in duration. The jump, in particular, was associated with a pulse train of four to eight pulses,