

## The evolution of the laterophysic connection with a revised phylogeny and taxonomy of butterflyfishes (Teleostei: Chaetodontidae)

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Accepted 2 June 2003

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### Abstract

The higher-level relationships of butterflyfishes were examined using 37 morphological characters. This analysis combines characters derived from a histological study describing variation in the morphology of the laterophysic connection (an association between the swim bladder and the lateral-line canals) with previously described morphological characters. The phylogenetic analysis resulted in four equally parsimonious trees that only differed in the placement of two of the 11 chaetodontid genera (*Amphichaetodon* and *Forcipiger*). We compare our analysis with previous hypotheses, present a new taxonomy consistent with the proposed cladistic relationships, and diagnose *Chaetodon* with five unreversed synapomorphies, including the evolution of characters composing the laterophysic connection. A new character-based diagnosis of *Chaetodon* is provided and species are allocated accordingly; *Chaetodon* now includes the former *Parachaetodon ocellatus* and excludes the former subgenera *Prognathodes* and *Roa*. The evolution of the laterophysic connection is examined by optimizing character-state transformations on the new hypothesis of relationships.

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### Introduction

Butterflyfishes are a widespread, diverse family of marine percoids with representatives on virtually all coral reef systems and in all tropical seas (Allen, 1980; Blum, 1989; Pyle 2001). Their bright and conspicuous color patterns have attracted much attention, generating a wealth of information about their behavior and ecology (e.g., Findley and Findley, 2001; Hourigan, 1989; Reese, 1975; Sano, 1989; Yabuta, 2002). However, studies of their phylogenetic relationships have not kept pace with studies of their ecology and behavior. This has resulted in chaetodontid taxonomies that do not provide diagnostic features for supraspecific taxa or recognize

monophyletic groupings (e.g., Allen et al., 1998; Burgess, 1978).

During the last 30 years, numerous authors have discussed butterflyfish taxonomy and relationships (Allen, 1980; Allen et al., 1998; Blum, 1988; Burgess, 1978; Maugé and Bauchot, 1984; Nalbant, 1971, 1973, 1986, 1991, 1995; Pyle, 2001), but the only explicit, phylogenetic analysis available has been the unpublished doctoral dissertation of Blum (1988; Fig. 1A). Blum's (1988) study was based largely on osteology and it included representatives of all nominal chaetodontid genera and subgenera established prior to 1988. Ferry-Graham et al. (2001) recently published a modified version of Blum's (1988) data matrix with an alternate coding and treatment of many of his characters as part of their study on the functional morphology and evolution of long jaws in butterflyfishes (Fig. 1B). This matrix included several problematic entries, and their

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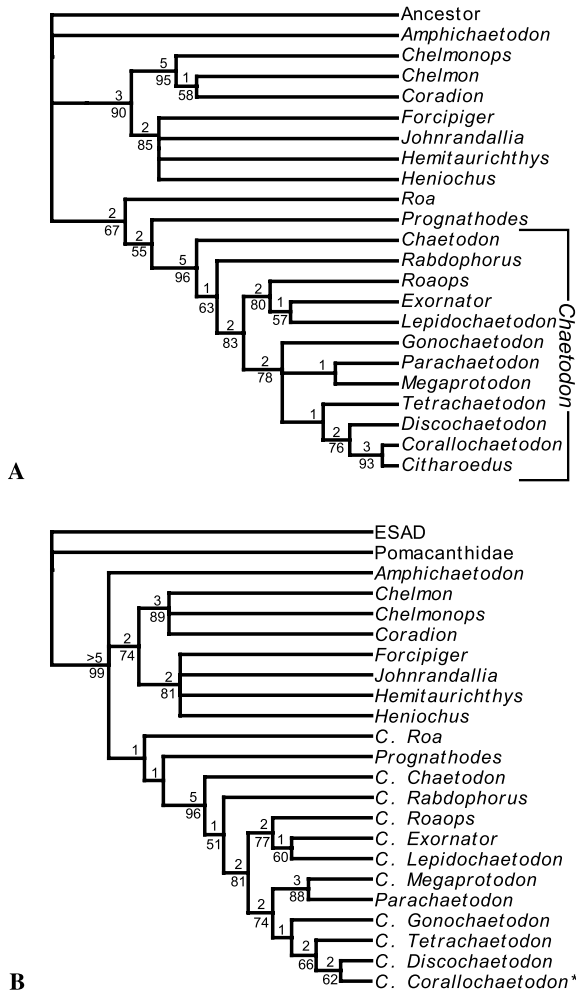


Fig. 1. The phylogenetic relationships of chaetodontid genera and *Chaetodon* subgenera hypothesized by previous studies. (A) The strict consensus cladogram of the 12 most parsimonious trees (tree length = 86 steps, CI = 0.65, RI = 0.86) resulting from the matrix of Blum (1988; his Fig. 34). (B) The strict consensus cladogram of the 10 most parsimonious trees (tree length = 83 steps, CI = 0.72, RI = 0.88) resulting from the matrix of Ferry-Graham et al. (2001 their Fig. 1b). Ferry-Graham et al. (2001) separated the ancestor of Blum (1988) into two outgroups: the Pomacanthidae as the first outgroup and the hypothetical ancestor of the ESAD as the second outgroup. Blum's (1988) subgenera *Corallochaetodon* and *Citharoedus* were combined into the subgenus *Corallochaetodon* by Ferry-Graham et al. (2001), so this synonymy is indicated by *Corallochaetodon*\*. All supraspecific taxa classified as *Chaetodon* subgenera by Ferry-Graham et al. (2001) are preceded by a "C." Bremer supports are listed above the branches and parsimony jackknife supports >50% are listed below the branches.

published taxonomy did not recognize monophyletic supraspecific taxa. Thus, butterflyfish taxonomy is becoming increasingly confusing, and an updated cladistic hypothesis of relationships and taxonomy are needed.

Blum (1988) suggested that skeletal morphology was approaching its limit for testing relationships among butterflyfishes. However, work by Webb (1998), Webb and Blum (1990), and Webb and Smith (2000) revealed interspecific variation in soft-tissue characters related to

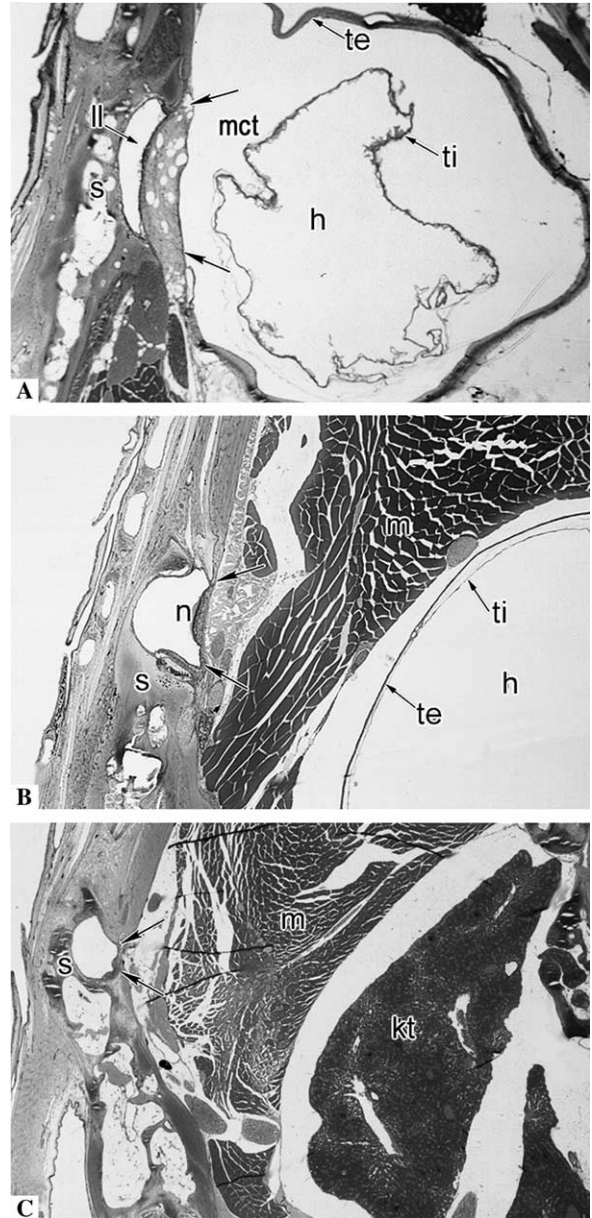


Fig. 2. Histological cross-sections of the direct and indirect laterophysic connections at the level of the supracleithrum. The left side of the images is lateral and the right side of the images is medial. (A) *C. octofasciatus* (uncataloged specimen) has a direct connection with mucoid connective tissue (mct). The laterophysic connection (arrows) is located in the incomplete medial wall of the lateral-line canal (ll) in the supracleithrum (s) and is a mechanical linkage between the fluid-filled lumen of the canal and the gas-filled horn (h) of the swim bladder. The horn is composed of the thick outer tunica externa (te) and the thin, epithelial tunica interna (ti). (B) *C. multinctus* (Cm4) has an indirect laterophysic connection with intervening muscle tissue (m) between the swim bladder horn and the fluid-filled lateral-line canal. The laterophysic connection (arrows) is located in the incomplete medial wall of the lateral-line canal in the supracleithrum. Both the tunica externa and tunica interna are present. Additionally, a neuromast (n) is located in this section. (C) *C. ornatissimus* (Cn4) has an indirect connection with reduced horns that do not reach the supracleithral lateral-line canal. Here, kidney tissue (kt) and muscle deep to the laterophysic connection (arrows) in the supracleithrum, but a swim bladder horn is not present at this level.

Blum's (1988) "pseudo-otophysic" connection in *Chaetodon*. Therefore, the present study coded these phylogenetically informative characters from a histological survey in *Chaetodon* and *Forcipiger*. Blum (1988) described this connection as a pair of antero-lateral diverticula ("horns") of the swim bladder that attach to the medially incomplete surface of each supracleithrum. He used this as a synapomorphy of his genus *Chaetodon*. Webb and Blum (1990) clarified the morphology of this feature using histological material, and Webb (1998) described two conditions, the "indirect" and "direct" types of laterophysic connections. The direct laterophysic connection, described in *Chaetodon octofasciatus*, is characterized by a "tympanum" that is found deep to the medial opening in the supracleithral lateral line canal and lateral to the gas-filled swim bladder horn (Figs. 2A and 3A). In contrast, the indirect laterophysic connection, described in *C. kleinii* and *C. sedentarius*, is characterized by the presence of epaxial musculature between the supracleithrum and the swim bladder horn that prevents direct contact between them (Figs. 2B and 3B). Webb and Smith (2000) established that the morphology of the laterophysic connection varies among, but not within, species, and Smith (2001) showed that variation in the morphology of the laterophysic connection is not correlated with mating strategies or feeding preferences. Because of the lack of a simple ecomorphological explanation for variation in the morphology of the laterophysic connection, Webb and

Smith (2000) and Smith (2001) hypothesized that laterophysic connection morphology may vary along lines of descent and provide phylogenetically informative characters. The present study clarifies the morphology of the laterophysic connection and describes additional variation found within it for an expanded set of *Chaetodon* species.

The goals of this paper are to: (1) propose a new hypothesis of higher-level chaetodontid relationships that combines the characters described from the laterophysic connection with previously coded morphological characters (Blum, 1988); (2) review recent hypotheses of chaetodontid relationships and taxonomies; (3) provide a taxonomy of butterflyfishes consistent with the cladistic relationships proposed herein; and (4) analyze the evolution of the laterophysic connection within *Chaetodon*.

## Materials and methods

### Specimen examination and preparation

Because of the large number of species in *Chaetodon* (87 species), a complete histological survey of laterophysic connection morphology was not feasible, so an ecologically and phylogenetically diverse subset of species was chosen for study. In particular, we focused our sampling efforts on the type species of Blum's (1988) *Chaetodon* subgenera. Forty-seven specimens (7.0–100 mm SL) representing 22 species of *Chaetodon* (25% of species and 92% of subgenera [as defined in the present study]) and one species of *Forcipiger* were examined histologically (Appendix A). All character states were invariant in each of the genera and subgenera proposed herein, except for the two species in the *Chaetodon* subgenus *Megaprotodon*, so these taxa were coded independently in the matrix. *Chaetodon striatus* also had a unique combination of characters, so it too was analyzed independently.

Institutional abbreviations follow Leviton et al. (1985) or refer to specimens in the private collection of J.F. Webb at Villanova University (e.g., Ca1, Co22). Specimens examined (Appendix A) include dry skeletons and material cleared and double stained for bone and cartilage (Pothoff, 1984). Live fishes were anaesthetized with MS 222 and immersion-fixed in 10% formalin in seawater following an injection of 10% formalin in seawater into the body cavity and/or head (following approved IACUC protocol).

Histological series were used to evaluate the morphology of the laterophysic connection and swim bladder. Fish heads were decalcified and dehydrated in an ascending ethanol series. Dehydrated tissue was embedded in glycol methacrylate resin (Historesin, Leica) and sectioned transversely or horizontally at 5 µm. Individual

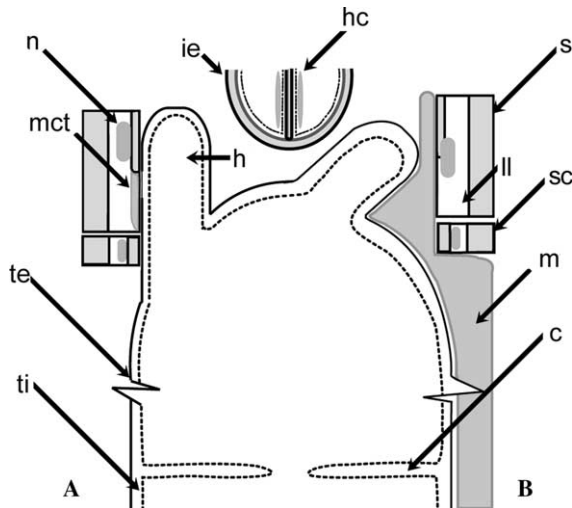


Fig. 3. Dorsal schematic representation of the direct and indirect laterophysic connections described by Webb (1998) based on the examination of histological cross-sections. (A) Direct connection with mucoid connective tissue tympanum (e.g., *C. octofasciatus*). (B) Indirect connection without mucoid connective tissue (e.g., *C. sedentarius*). Abbreviations: c, internal sphincter; h, swim bladder horn; hc, inner ear hair cell; ie, inner ear; ll, lateral-line canal; m, muscle tissue; mct, mucoid connective tissue tympanum; n, neuromast; s, supracleithrum; sc, lateral-line scale; te, tunica externa of swim bladder; ti, tunica interna of swim bladder.

sections were mounted onto plain or chrom-alum subbed slides and dried overnight at 60 °C, stained with 0.5% cresyl violet, air-dried, and coverslipped.

### *Phylogenetic methods*

In order to examine chaetodontid relationships, 41 characters (37 informative) were analyzed (Appendices B and C) with all transformations weighted equally. Characters 1–7 and 10–35 are taken directly from Blum (1988), and the character states are based solely on the specimens he examined (see Appendix D). Character states for characters 36–40 are based solely on the species examined histologically (Appendices A and D). The character states for characters 8, 9, and 41 are based on the specimens examined by Blum (1988) and the species examined histologically in the current study. Blum's character 34, the presence or absence of a large semicircular posterior lamina in the posttemporal, was removed following the examination of additional taxa (by SDB) that indicated that the original observation was incorrect. All chaetodontid character states were invariant within the terminals (usually genera or *Chaetodon* subgenera) coded in the matrix. Thirty-one characters were coded into binary states and 10 characters were coded into multistates. We did not infer the sequence of transformations for character 16, so this character was treated non-additively (unordered). The remaining nine multistate characters (1, 2, 4, 10, 18, 19, 21, 26, and 34) were arranged in the transformation series hypothesized and justified by Blum (1988). Many authors have argued against using additive (ordered) characters because they represent hypotheses of character evolution that should be tested by the analysis, not assumed (e.g., Ferry-Graham et al., 2001; Hauser and Presch, 1991; Wilkinson, 1992). However, we follow Mickevich (1982) who pointed out that non-additive multistate characters appear superficially to avoid premises of transformation, but in reality, they assume a different, questionable hypothesis of transformation. Additionally, Lipscomb (1992) and Pimentel and Riggins (1987) have argued that analyses using exclusively non-additive multistate characters ignore observed information about nested character similarity, which is equivalent to ignoring evidence, and is invalid in cladistic analyses.

Despite the general acceptance of character optimization as a valid method for examining character evolution, there has been a debate about whether or not to include the characters under examination in the phylogenetic analyses. Many authors (e.g., Brooks and McLennan, 1991; Coddington, 1988) have argued that there are problems of circularity, dependence, and bias when characters under examination are included in the phylogenetic analysis. Kluge and Wolf (1993) and Wenzel (1997) have argued that the exclusion of any characters necessarily leads to weaker phylogenetic

hypotheses and that the concerns over circularity and dependence are unfounded. Following the argumentation presented in Kluge and Wolf (1993) and Wenzel (1997), we examined the evolution of laterophysic connection by optimizing character transformations on the topology constructed using all informative characters because this hypothesis represents the least refuted hypothesis of relationships for the family. Additionally, we used unambiguous changes common to all most parsimonious dichotomized trees to diagnose clades (instead of an optimization of characters on the strict-consensus tree; following Goloboff, 1995).

The character data used in these analyses were edited and viewed in WinClada (Nixon, 1999). All autapomorphic characters were included in character descriptions, but were removed before analyses. Phylogenetic analyses were run using NONA (Goloboff, 1999) using 1000 replications with different random addition sequences of taxa. Each replication began with an initial Wagner tree followed by TBR (tree bisection and reconnection) branch swapping, keeping up to 10 trees per replication. All resulting trees were then submitted to a final round of TBR branch swapping (command sequence: h/10;rs0;mult\*1000;max\*);).

Levels of nodal support for analyses were examined in NONA with Bremer indices (Bremer, 1994) and parsimony jackknifing (Farris et al., 1996). After converting the additive characters to additive binary coding (Farris et al., 1970), jackknife analyses (1000 replications, 10 random addition replicates per replication, TBR branch swapping) were analyzed through WinClada. Additive binary coding was used because jackknife analyses using additive multistate characters in a non-additively binary coded matrix may underestimate jackknife support (J. Faivovich and T. Grant, pers. comm.). The matrices of Blum (1988) and Ferry-Graham et al. (2001) were both re-analyzed using parsimony jackknifing and Bremer indices for comparison with our matrix.

### *Data matrix*

Blum (1988) analyzed the relationships of several deep-bodied perciform families or "higher squamipennes" to examine the interrelationships of the Chaetodontidae. In this analysis, he coded 36 binary characters with equal weights and a 37th character with a weight of 11 (for the 11 synapomorphies listed by Tyler et al. (1989) uniting the siganids and the acanthurids) for 12 terminals: hypothetical percoid ancestor, *Kyphosus*, *Microcanthus*, Scatophagidae, Siganidae, Acanthuridae, *Drepane*, *Chaetodipterus*, *Platax*, *Rhinoprenes*, Pomacanthidae, and Chaetodontidae. This analysis resulted in two equally most parsimonious trees of 63 steps [although Blum (1988, p. 56) reported 64 steps; Fig. 4]. He hypothesized that the Pomacanthidae was the sister group of the Chaetodontidae based on three characters:

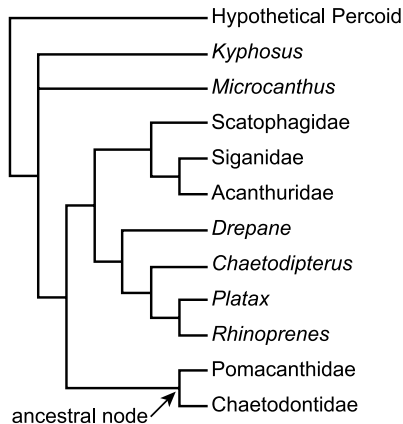


Fig. 4. Phylogenetic relationships among selected deep-bodied percoids or “higher squamipennes” from Blum (1988). The arrow points to the node used in Blum (1988) and in this study as the hypothetical ancestor of the Chaetodontidae.

the organization of tooth replacement and the distribution of jaw teeth; the reformed optic foramen; and the reduced pharyngobranchials. The clade, Chaetodontidae + Pomacanthidae, was sister to the clade (((Scatophagidae + (Siganidae + Acanthuridae)) + (*Drepane* + Ehippidae))) based on three characters: presence of comma-shaped tooth patches on the pharyngobranchials; six or fewer branchiostegal rays; and the opercular membranes attached to the isthmus, rather than each other. The interrelationships of this clade with *Kyphosus* and *Microcanthus* were left unresolved in a polytomy.

Blum (1988) used this phylogenetic hypothesis of higher squamipennes to construct a hypothetical ancestor for his analysis of chaetodontid intrarelationships. To generate this ancestor, he optimized the character states of all characters in his chaetodontid analysis on this outgroup topology. The reconstruction of these characters at the first outgroup node (arrow in Fig. 4) was used to root his analysis of chaetodontid intrarelationships. For all characters taken from Blum (1988), we have retained the coding of his hypothetical ancestor. For new and modified characters, we reconstructed the ancestral state, when applicable, using the data in Blum (1988) and observations from the pomacanthid *Pomacanthus navarchus*. Blum (1988) described six characters that diagnose a monophyletic Chaetodontidae: (1) sequential articulation between the first dorsal pterygiophore, the supraneural bones, and the supraoccipital crest; (2) pleural rib laminae that extend forward from the medial edges of the descending shafts; (3) pleural ribs of exceptional length; (4) presence of a ligament that connects the anterior edge of the second post-cleithrum to the basipterygium, just anterior to the origin of the pelvic spine; (5) the two anterior branchiostegals (or, if only five are present, the single anterior branchiostegal) do not make contact with the ceratohyal; (6) specialized larval stage known as a tholichthys larva. This sixth character, the presence of a tholichthys larval stage

(sensu Burgess, 1978), has been questioned by some authors (e.g., Leis, 1989) because some chaetodontids do not share the typical tholichthys form and some non-chaetodontids (e.g., scatophagids) have similar larval morphology. Regardless of the utility of using the tholichthys larval stage as a synapomorphy of the family, the monophyly of the family is still supported by the first five characters presented above. Based on the evidence provided by Blum (1988) and summarized above, the monophyly of the Chaetodontidae was assumed, and the hypothetical ancestor was used to root the tree.

The character matrix (Appendix B) includes 24 terminals: the hypothetical ancestor to the Chaetodontidae, the 10 non-*Chaetodon* butterflyfish genera recognized by Blum (1988), the 11 *Chaetodon* subgenera recognized in this study, with two species in the *Chaetodon* subgenus *Megaprotodon* (*Chaetodon oligacanthus* and *C. trifascialis*), and a separate *Chaetodon striatus*.

## Results

### Character descriptions from Blum (1988)

Thirty characters (labeled B in Appendix C) were taken directly from Blum (1988) with two minor modifications. (1) Following Mabee (1988), predorsal bones are referred to as supraneural bones (character 2). (2) Histological examination of *Chaetodon* (*Tetrachaetodon*) *plebeius* revealed that this species had an external swim bladder constriction. Therefore, this condition was also examined in cleared and stained specimens of *Chaetodon* (*Tetrachaetodon*) *speculum*. Both species had an external swimbladder constriction so the condition for the subgenus *Tetrachaetodon* was recoded as being present (character 9).

### Newly described characters or those altered from Blum (1988)

**Character 8.** Presence of swim bladder horns. All *Chaetodon* species examined by Blum (1988) and in this study have swim bladder horns. The non-*Chaetodon* butterflyfishes examined by Blum (1988) and the angelfish *P. navarchus* lack swim bladder horns.

**Characters 25–26 and 34–35.** Palato-palatine ligament (25) and the apophysis on the palatine’s maxillary process (26). Blum (1988) originally coded these two characters as part of a single multistate character with three states. Here, these characters are split into two binary characters, separating the development of an apophysis on the palatine maxillary process from the origination of the palato-palatine ligament because of the potential for independence. Similarly, the palato-vomerine ligament (34) and the apophysis at the insertion of the vertical palato-vomerine ligament (35) were separated into two

binary characters instead of the single multistate character described in Blum (1988).

**Character 36.** Type of laterophysic connection. Webb (1998) described the indirect laterophysic connection in *Chaetodon sedentarius* and *C. kleinii*. This condition is also found in all species examined histologically in the *Chaetodon* subgenera *Chaetodon*, *Exornator*, *Lepidochaetodon*, *Corallochaetodon*, and *Citharoedus* and is characterized by the presence of epaxial musculature deep to the medially incomplete supracleithral lateral-line canal (Figs. 2B, C and 3B). A direct laterophysic connection, first described by Webb (1998) in *C. octofasciatus* (Figs. 2A and 3A), is also seen in *C. striatus* and all species examined histologically in the *Chaetodon* subgenera *Discochaetodon*, *Gonochaetodon*, *Megaprotodon*, *Rabdophorus*, and *Tetrachaetodon*. The direct laterophysic connection is characterized by the swim bladder horn deep to the medially incomplete supracleithrum without intervening muscle tissue.

**Character 37.** Swim bladder-peritoneal relationship. Both non-*Chaetodon* taxa examined (*P. navarchus* and *Forcipiger flavissimus*) and all species examined histologically in the *Chaetodon* subgenera *Citharoedus*, *Corallochaetodon*, *Exornator*, and *Lepidochaetodon* have a swim bladder with a tunica externa that is thin dorsally and thicker ventrally. The swim bladder in these species is positioned dorsal to a thick peritoneum, which is tightly attached to the ribs in the lateral wall of the body. This swim bladder morphology is defined as an “attached swim bladder.” In contrast, *Chaetodon striatus* and all species examined histologically in the *Chaetodon* subgenera *Chaetodon*, *Discochaetodon*, *Gonochaetodon*, *Megaprotodon*, *Rabdophorus*, and *Tetrachaetodon* have a swim bladder with a uniformly thick tunica externa. The swim bladder in these subgenera is covered by a thin, translucent peritoneum, and the caudal end of the swim bladder appears to be sitting free in the body cavity. This is defined as a “free swim bladder.”

**Character 38.** Width of swim bladder horns. Blum (1988) described narrow swim bladder horns in *C. oligacanthus* and *C. trifascialis*. We confirm Blum’s findings for these two species and we show, using histological analysis, that contrary to Blum (1988), *C. plebeius* has narrow horns. This suggests that all species in the *Chaetodon* subgenus *Tetrachaetodon* (to which *C. plebeius* belongs) are likely to have narrow swim bladder horns. These narrow swim bladder horns are similar in diameter to the supracleithral lateral-line canal; in one specimen of *C. plebeius* (Cp2) the horn actually invades the supracleithrum through the medial opening. All other *Chaetodon* species that were examined histologically have comparatively wide swim bladder horns with diameters that are more than two times the diameter of the supracleithral lateral-line canal.

**Character 39.** Length of swim bladder horns. Webb and Smith (2000) described the condition in the

*Chaetodon* subgenus *Citharoedus*, which is characterized by small antero-dorsally directed horns on the anterior end of the swim bladder that barely separate from the body of the swim bladder. The swim bladder horns in the *Citharoedus* species examined histologically do not reach the level of the medial opening in the supracleithral lateral-line canal (Fig. 2C). All other *Chaetodon* species examined histologically have longer swim bladder horns that extend rostrally beyond the level of the medial opening in the supracleithral lateral-line canal.

**Character 40.** Presence of mucoid connective tissue (MCT, stains pink with cresyl violet), located deep to the supracleithral lateral-line canal (Fig. 5). Webb

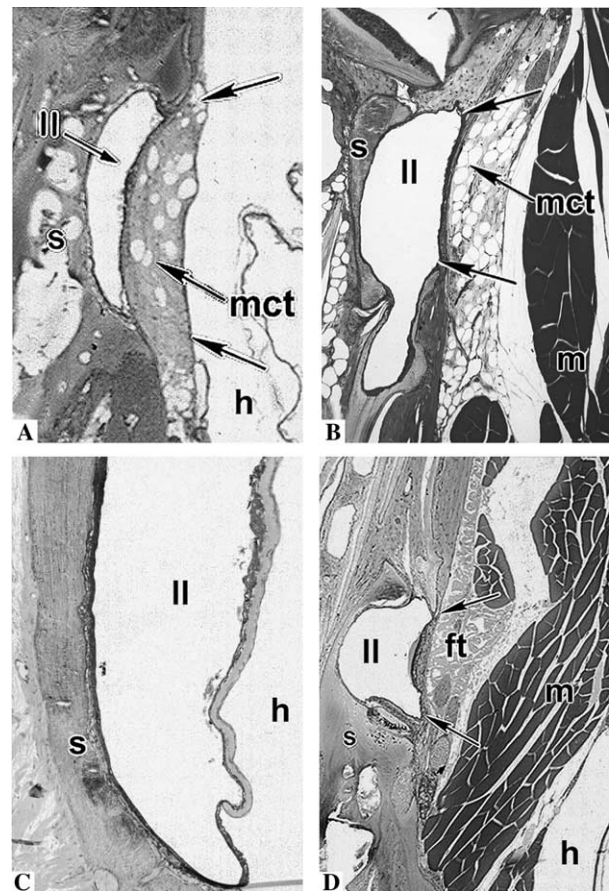


Fig. 5. Histological cross-sections at the level of the supracleithrum comparing the intervening tissues associated with the laterophysic connection. The left side of the images is lateral and the right side of the images is medial. (A) *C. octofasciatus* (uncataloged specimen) has a direct laterophysic connection (arrows) with mucoid connective tissue (mct) deep to the lateral-line canal (ll) in the supracleithrum (s) and lateral to the swim bladder horn (h). (B) *C. kleinii* (Ck10) has an indirect laterophysic connection (arrows) with mct deep to the lateral-line canal in the supracleithrum and muscle tissue (m) lateral to the swim bladder horn. (C) *C. plebeius* (Cp1) has a direct laterophysic connection without mct between the lateral-line canal in the supracleithrum and the swim bladder horn. (D) *C. multinctus* (Cm4) has an indirect laterophysic connection without mct between the lateral-line canal in the supracleithrum and fatty tissue (ft) lateral to the muscle layer (m) that is lateral to the swim bladder horn.

(1998) described the presence of MCT as an important feature of the tympanum in the direct laterophysic connection in *C. octofasciatus* (Fig. 5A). This condition is also seen in *C. striatus* and all species examined histologically in the *Chaetodon* subgenera *Discochaetodon*, *Gonochaetodon*, and *Rabdophorus*. All species examined histologically in the *Chaetodon* subgenus *Lepidochaetodon* have an indirect laterophysic connection with MCT present (Fig. 5B). All species examined histologically in the *Chaetodon* subgenera *Megaprotodon* and *Tetrachaetodon* have a direct laterophysic connection, but lack MCT (Fig. 5C). Finally, all species examined histologically in the *Chaetodon* subgenera *Chaetodon*, *Exornator*, *Corallochaetodon*, and *Citharoedus* and *F. flavissimus* lack MCT deep to the supracleithral lateral-line canal (Fig. 5D).

**Character 41.** Condition of the supracleithral lateral-line canal. Blum (1988) described a medially incomplete

supracleithrum as part of his pseudo-otophysic connection character. The medial opening (= medial fossa of Webb, 1998) actually represents the posterior terminal pore of the lateral-line canal contained in the supracleithrum. The lateral-line canal is open both rostrally and caudally, but its posterior terminal pore is directed medially, and is not a novel fossa. All *Chaetodon* species examined have a medially incomplete supracleithral lateral-line canal (Fig. 6). In contrast, *F. flavissimus* has an enclosed, medially complete supracleithral lateral line canal that terminates at the posterior end of the supracleithrum, confirming Blum's (1988) observation that non-*Chaetodon* butterflyfishes have a medially complete supracleithrum.

#### Phylogenetic analysis

The analysis resulted in four most parsimonious trees, length 92 steps, consistency index (CI; Kluge and Farris, 1969) 0.58, and retention index (RI; Farris, 1989) 0.85 (Fig. 7). The strict consensus of the four most parsimonious trees is presented in Fig. 8. The only differences among the four most parsimonious trees are the placement of *Amphichaetodon* and the placement of *Forcipiger* as either the sister taxon of *Hemitaurichthys* or as the sister taxon of *Johnrandallia* + (*Hemitaurichthys* + *Heniochus*) (Fig. 7).

Parsimony jackknifing and Bremer indices suggest that most of the nodes resulting from the analysis are well supported. Jackknife support exceeded 50% in 13 of 18 nodes and exceeded 70% in 9 of 18 nodes found in the strict consensus tree (Fig. 8). In general, relationships with high Bremer support were better supported by parsimony jackknifing. Nine nodes resulting from the analysis have Bremer supports  $\geq 2$  and five nodes have Bremer support  $\geq 3$  (Fig. 8). The genus *Chaetodon* had the most support with a Bremer support value of 6; it was diagnosed by five unique synapomorphies (characters 2, 8, 31, 32, and 41) and one additional synapomorphy (a reversal of character 23), providing strong evidence of its monophyly. Many nodes were well supported, and not surprisingly, jackknife and Bremer supports were highest in clades diagnosed by multiple unique synapomorphies.

#### Discussion

##### *The phylogeny of butterflyfishes*

##### *Past studies*

Burgess (1978) provided the most widely recognized hypothesis of chaetodontid relationships. Nalbant's series of papers (1971, 1973, 1974, 1984, 1986, 1991, 1995) on butterflyfish relationships has added to our understanding of chaetodontid morphology, but the

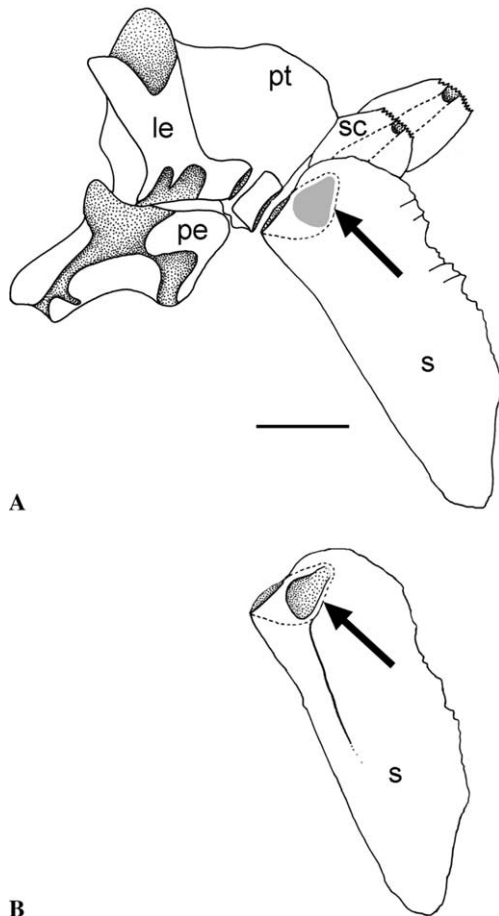


Fig. 6. Camera lucida illustration of the laterophysic connection (arrow) and associated skeletal structures. (A) Lateral view of the left side of the posterior margin of the skull in *C. octofasciatus* (AMNH 43117). Lateral-line canal of supracleithrum (s) marked with dashed line. Laterophysic connection (only visible from medial surface) shown in grey. (B) Schematic representation of medial surface of the right supracleithrum and laterophysic connection based on *C. octofasciatus* (AMNH 43117). Abbreviations: le, lateral extrascapular; pe, pterotic; pt, posttemporal; sc, first lateral-line scale.

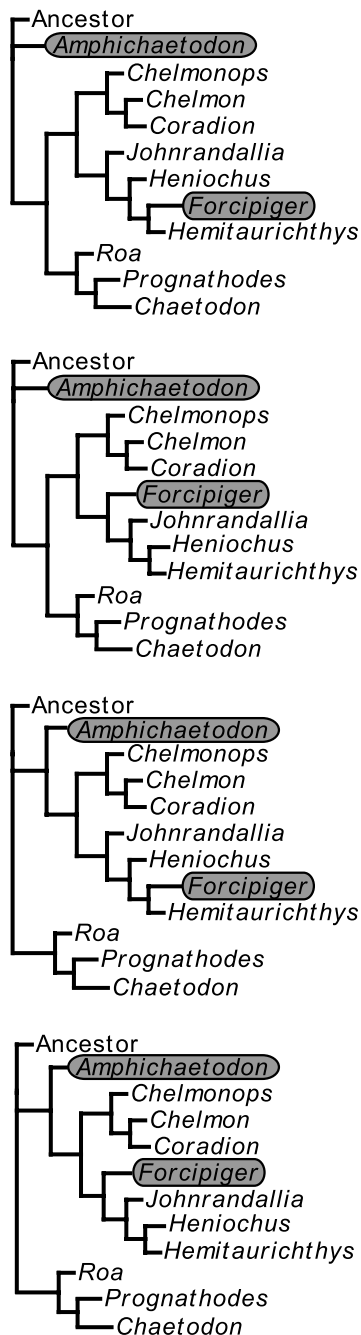


Fig. 7. Four most parsimonious trees resulting from the analysis of chaetodontid relationships (tree length = 92 steps, CI = 0.58, RI = 0.85). *Amphichaetodon* and *Forcipiger* are the only taxa whose relationships change in the four cladograms, so they are highlighted in grey. The subgeneric relationships within *Chaetodon* are identical in all four trees and are shown in the strict consensus tree in Fig. 8.

relationships presented in these papers have not been readily accepted. One reason for this may be Nalbant's continued view that "plesiomorphies are extremely important in establishing the phylogeny of a group" (Nalbant, 1995, p. 506). Recently, Allen et al. (1998) presented an updated classification of butterflyfishes. The most notable change was the recognition of *Prog-*

*nathodes* as a genus separate from *Chaetodon*. All of these hypotheses have relied on non-cladistic, evolutionary methods for resolving relationships, and did not recognize monophyletic supraspecific taxa. Maugé and Bauchot (1984) provided a phenetic hypothesis of chaetodontid relationships that has not been generally accepted. Blum (1988) provided the first hypothesis of relationships for the Chaetodontidae based on cladistic methods (Fig. 1A), but the matrix remained unpublished until Ferry-Graham et al. (2001) published an analysis based on a modified version of his data.

Ferry-Graham et al. (2001) re-analyzed Blum's (1988) data matrix after treating all of Blum's additive multistate characters as non-additive multistate characters, separating Blum's hypothetical ancestor into two separate composite taxa (Pomacanthidae and ESAD [composed of the Ehippidae, Scatophagidae, Acanthuridae, and *Drepane*]), and recoding Blum's question marks with new apomorphic character states. Several features of the Ferry-Graham et al. (2001) analysis warrant a critical review. In general, their re-analysis did not alter Blum's (1988) relationships appreciably, but it did result in a loss of resolution among genera and more resolution, but less support, among *Chaetodon* subgenera (Fig. 1). Note that Ferry-Graham et al.'s (2001, Fig. 1A) which is meant to represent the phylogeny of Blum (1988), reports the incorrect relationships. According to Blum (1988), *Discochaetodon*, not *Tetrachaetodon*, is the sister group of *Corallochaetodon* + *Citharoedus*. The correct relationships are shown in Blum's (1988, Fig. 34), Blum's (1989) Fig. 1, and our Fig. 1A.

By treating all of Blum's (1988) additive multistate characters non-additively, Ferry-Graham et al. (2001) reported a loss of resolution in some clades. For example, their character 15 (our character 18) describing jaw and tooth morphology, the focus of their study, was assigned nine character states. Of these, four (including a ninth state that they added for *Forcipiger*) are autapomorphic and uninformative when non-additively coded. Their analysis could have broken up and recoded the jaw and teeth features using data provided by Blum (1988) and the data described in their study if they had preferred not to use additive coding. However, coding the character as nine non-additive states, their analysis significantly reduced the information content of this character. Additionally, Ferry-Graham et al.'s (2001) unordering was incomplete; their analysis did not code additional character states described in the text by Blum (1988) that were omitted from his matrix because they were autapomorphic. Blum (1988) had excluded autapomorphic character states (e.g., character states in the *Chaetodon* subgenera *Citharoedus* and *Lepidochaetodon* for character one [the condition of the first dorsal pterygiophore]) from his matrix because they were uninformative in an additively binary coded analysis. However, these character states cannot be excluded



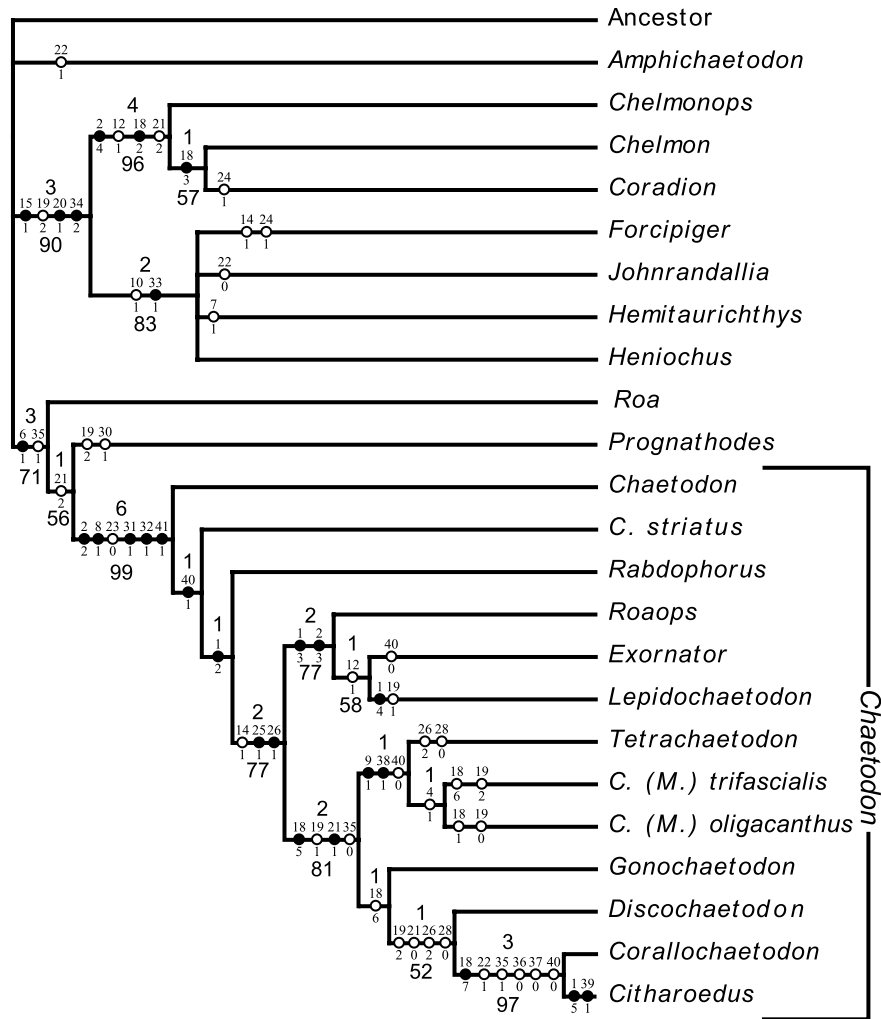


Fig. 8. Strict consensus of the four most parsimonious trees (shown in Fig. 7) resulting from the analysis of chaetodontid generic and subgeneric relationships (tree length = 92 steps, CI = 0.58, RI = 0.85). Synapomorphies common to all four most parsimonious trees are listed before the node. Unreversed synapomorphies are depicted as black circles and non-unique synapomorphies are depicted as open circles. Additionally, autapomorphies in terminal taxa that were excluded from the analysis are shown as optimized on the cladogram. Character numbers (above each circle) represent the character numbers listed in Appendix C with character states below the circle. Bremer supports are listed above the branches and parsimony jackknife supports >50% are listed below the branches.

from a non-additively coded analysis because each taxon must be coded with its homologous character state.

Ferry-Graham et al. (2001) eliminated all question marks from Blum's (1988) matrix to avoid the problems with missing data (Maddison, 1993; but see Kearney, 2002). However, the question marks coded in Blum's (1988) hypothetical ancestor did not represent missing data, but represented an equivocal state at the first outgroup node based on the reconstruction of the chaetodontid characters on the outgroup topology. Additionally, Ferry-Graham et al. (2001) coded new apomorphic character states for chaetodontid terminals with question marks with the justification that this could "increase character resolution" (p. 122). However, some of their replacement character states were not well founded. For example, their character 22 (the condition

of the palato-palatine ligament [PPL] and apophysis) was described in *C. oligacanthus* (their *Parachaetodon ocellatus*) as "originally coded as having state 1 in Blum's matrix (1988) but coded as unknown for character state 2" in a new apomorphic character state 3 (Ferry-Graham et al., 2001, p. 143). Creating this new autapomorphic character state is problematic because it does not describe the condition of the PPL and apophysis in *C. oligacanthus*. Unknown character states should only be replaced by homologous character states derived from the examination of specimens or from the literature, not with non-descriptive apomorphic states. As Kearney (2002) stated, resolution is a goal of phylogenetic analysis, but it should not come at the cost of using methods that imply more resolution than the data support.

### Current study

The strict-consensus cladogram resulting from the analysis presented here is more resolved than the cladograms of Blum (1988; Fig. 1A) or Ferry-Graham et al. (2001; Fig. 1B), even though Jackknife and Bremer supports for our phylogenetic hypothesis (Fig. 8), the hypothesis of Blum (1988; Fig. 1A), and the hypothesis of Ferry-Graham et al. (2001; Fig. 1B) are similar. The inclusion of the characters described herein and those modified from Blum (1988) increases character support for some of the nodes originally recognized by Blum (1988) (e.g., *Chaetodon*), places the *Chaetodon* subgenus *Tetrachaetodon* as the sister group to *Megaprotodon* (his *Megaprotodon* + *Parachaetodon*), and places the subgenus *Gonochaetodon* as the sister group of *Discochaetodon* + (*Corallochaetodon* + *Citharoedus*).

### The taxonomy of butterflyfishes

#### Past studies

Historically, chaetodontid taxonomy has received a substantial amount of taxonomic attention (reviewed in Burgess, 1978). Burgess (1978) also provided the framework for most modern taxonomies (Blum, 1988). However, the consensus among systematists concerning the taxonomy of this group has been declining. The four major recent taxonomies disagree on generic and subgeneric assignments in about two thirds of the species (see Appendix D). Only 8 of 87 *Chaetodon* species (as classified in this study) were placed in *Chaetodon* by all authors. Contrary to the taxonomy of Blum (1988) and the taxonomy presented here, Allen (1980), Allen et al. (1998), Burgess (1978), Maugé and Bauchot (1984), and Nalbant (1971, 1973, 1986, 1991, 1995) published taxonomies that did not provide evidence of monophyly for supraspecific taxa and were not based on cladistic hypotheses of relationships. Blum (1988) was the first to use cladistic methods to generate a butterflyfish taxonomy. His survey of the osteology in 86 species (57 cleared and stained and 29 radiographed) in all 22 supraspecific taxa recognized by Burgess (1978) recognized 120 species in 11 genera in the Chaetodontidae, including 83 species in *Chaetodon*, which he divided into 12 subgenera. Blum (1988, 1989) synonymized the monotypic *Parachaetodon* with *Chaetodon* and resurrected the oldest available name, *C. oligacanthus* Bleeker, 1850, for *P. ocellatus* (Cuvier, 1831) to avoid creating a secondary homonym of the Caribbean species *Chaetodon ocellatus* Bloch, 1787. In the most recent review and taxonomy of butterflyfishes, Allen et al. (1998) recognized 122 species, of which 88 were included in 12 *Chaetodon* subgenera. Notably, only half of the *Chaetodon* subgenera in Allen et al. (1998) and Blum (1988) were composed of the same, or nearly the same species, indicating very different subgeneric taxonomies.

In an attempt to reconcile the results of their phylogenetic analysis with the taxonomy of Allen et al. (1998), Ferry-Graham et al. (2001) recognized a paraphyletic *Chaetodon*. The genus *Roa* was recognized as a *Chaetodon* subgenus, although it was the sister group of their *Prognathodes* + *Chaetodon*, and *C. oligacanthus* (their *P. ocellatus*) was classified as a monotypic genus, although it was nested within *Chaetodon* in their analysis (Fig. 1B). They also synonymized the *Chaetodon* subgenus *Citharoedus* with *Corallochaetodon*, because these taxa were “identical in all character states” (Ferry-Graham et al., 2001, p. 141), although *Citharoedus* has priority. Blum’s (1988) character matrix did not include autapomorphies (see discussion above), so these two subgenera were coded with identical character states. However, these two subgenera should not be synonymized because there are both skeletal and soft tissue characters supporting the monophyly of each (Blum, 1988, p. 236; present study).

#### Current study

The cladistic analysis presented here provides an opportunity to clarify several longstanding problems in the “traditional” butterflyfish taxonomy, including the recognition of a monophyletic *Chaetodon* diagnosed by the presence of six synapomorphies (five unreversed). The taxonomy presented here includes the species recognized by Blum (1988) with seven additional species and one synonymy (Appendix D). We include four species described after 1988: *Chaetodon andamanensis* from the eastern Indian Ocean (Kuiter and Debelius, 1999), *C. dialeucos* from the Arabian Sea (Salm and Mee, 1989), *Prognathodes brasiliensis* from southern Brazil (Burgess, 2001), and *P. carlhubbsi* from the Galapagos (Nalbant, 1995). Three *Chaetodon* subspecies (sensu Burgess, 1978) are recognized as full species based on the arguments and characters presented by Gill (1999) for the specific recognition of well-diagnosed geographic forms: *Chaetodon interruptus* (also following Allen et al., 1998), *C. humulatus* (also following Kuiter, 1995), and *C. pictus*. We have classified these seven species (based on similarity) using the information given in their original descriptions and subsequent species accounts. Following McMillan et al. (1999), we have synonymized *C. pelewensis* with *C. punctatofasciatus*. Thus, we recognize 126 species of chaetodontids (Appendix D).

Blum’s (1988) *Chaetodon* subgenus *Chaetodon*, which includes *C. striatus*, shows variation in laterophysic connection morphology, but we found no other evidence to refute the monophyly of Blum’s supraspecific taxa. Of the taxa not diagnosed with apomorphic characters (Fig. 8), only the genus *Roa* and the *Chaetodon* subgenera *Chaetodon* and *Rabdophorus* lacked evidence for monophyly in Blum’s dissertation. Blum (1988) found no osteological features that unambiguously diagnose the genus *Roa*. Because these species do not have swim bladder horns, we did not examine them. Therefore, we

retain Blum's (1988) composition and taxonomy until evidence suggests otherwise.

Blum (1988) could not diagnose the subgenus *Rabdophorus*, but found no variation in skeletal anatomy among species placed in this subgenus. This study found no variation in their laterophysic connection morphology as a first, albeit limited, test of its monophyly. Blum (1988) could not find any osteological differences between species in Burgess's (1978) subgenera *Rabdophorus* and *Chaetodontops*, so he synonymized them, but there is evidence from color pattern that multiple species groups may be present. We retain Blum's (1988) taxonomy until these species can be separated as the result of further cladistic analyses. Similarly, Blum (1988) did not find apomorphic features for his *Chaetodon* subgenus *Chaetodon*. Two species in this subgenus, *C. capistratus* and *C. ocellatus*, have an indirect laterophysic connection (character 36) with no mucoid connective tissue (character 40) while *C. striatus*, another species in Blum's subgenus *Chaetodon*, has a direct laterophysic connection with mucoid connective tissue present. The remaining species in this subgenus (*C. hoefleri*, *C. humeralis*, *C. marleyi*, and *C. robustus*) were not examined in this study, and Blum (1988) did not examine their osteology (except for a radiograph of *C. hoefleri*). Thus, we leave six species (Appendix D) in the subgenus *Chaetodon* following Blum (1988) and Burgess (1978), but remove *C. striatus* from this subgenus because of its unique combination of characters, which would have rendered the subgenus *Chaetodon* (sensu Blum, 1988) non-monophyletic.

Bleeker (1877, p. 312) and Burgess (1978, p. 306) listed *C. striatus* as the type species of the *Chaetodon* subgenus *Tetragonopterus*. However, *C. striatus* is not available as the type of *Tetragonopterus*. This is because the first usage of *Tetragonopterus*, which is consistent with the criteria of availability, is found in Bleeker (1873, p. 140) where he describes nine species of butterflyfishes in *Tetragonopterus*. However, *Chaetodon striatus* was not one of the species listed in *Tetragonopterus* in that publication. It is not, therefore, available to be the type of that name, despite Bleeker's and other author's subsequent listings (Bleeker, 1877; Burgess, 1978; Jordan, 1963) as such. No other genus group name was found for which *C. striatus* could be considered as the type species, so we leave this species as *incertae sedis* until more work on a *Chaetodon* species-level phylogeny, particularly in the subgenera *Chaetodon* and *Rabdophorus*, resolves the position of *C. striatus* relative to its congeners.

In summary, our taxonomy follows Blum (1988) except for the recognition of seven additional species, the synonymy of *C. pelewensis* with *C. punctatofasciatus*, the separation of *C. striatus* from the remainder of the *Chaetodon* subgenus *Chaetodon*, and the synonymy of his *Chaetodon* subgenera *Megaprotodon* and *Parachaeatodon* (because both monotypic subgenera were resolved as sister-species in our analysis).

### *Evolution of the laterophysic connection in Chaetodon*

Our study describes or redefines several phylogenetically informative characters associated with the laterophysic connection, a novel association of paired swim bladder horns with the medial opening of the supracleithral lateral-line canal. The resulting character-state transformations were optimized on our hypothesis of relationships to examine patterns in its evolution (Fig. 8).

The presence of swim bladder horns and the medially incomplete supracleithrum were described by Blum (1988) as the most substantial modification of internal anatomy known to occur in the family. These two structures (characters 8 and 41, respectively) define the laterophysic connection described by Webb (1998) and Webb and Blum (1990) and are optimized at the basal node in *Chaetodon*. Additionally, these results suggest that the ancestor of *Chaetodon* had the free swim bladder condition (character 37). Character 37 transforms to the attached swim bladder condition in *Corallochaetodon* + *Citharoedus* and in *Exornator* + *Lepidochaetodon*. The condition for the subgenus *Roaops* is unknown. The type of laterophysic connection (character 36) reverses from a direct laterophysic connection to an indirect laterophysic connection in *Exornator* + *Lepidochaetodon* and in *Corallochaetodon* + *Citharoedus*. The subgenus *Chaetodon* has an indirect laterophysic connection, and the condition in the subgenus *Roaops* is unknown. Thus, this analysis shows that the direct laterophysic connection is found only in some members of the large clade that is the sister group to the subgenus *Chaetodon*. Interestingly, the pattern of gains and losses is similar for the mucoid connective tissue deep to the supracleithrum (MCT, character 40). Mucoid connective tissue is primitively absent in *Chaetodon*; it evolved only once in the same large clade as the direct laterophysic connection. It was then lost in the ancestor of *Corallochaetodon* + *Citharoedus* and *Exornator*. The pattern of simultaneous reversals in swim bladder morphology, mucoid connective tissue (except *Lepidochaetodon*), and laterophysic connection type in two *Chaetodon* clades (*Lepidochaetodon* + *Exornator* + (*Roaops*?) and *Corallochaetodon* + *Citharoedus*, Fig. 8) suggests that these characters may contribute to the functional evolution of the laterophysic connection. Interestingly, the short horns (character 39) are found only in *Citharoedus* and are likely the result of a heterochronic reduction in horn length. Finally, narrow swim bladder horns (character 38) and the presence of an external constriction of the swim bladder (character 9) are both derived characters in *Tetrachaetodon* + *Megaprotodon*, the only taxa with a direct laterophysic connection that lacks MCT (character 40). Future studies of the behavioral and functional roles of the laterophysic connection can now be explored in the context of this evolutionary hypothesis.

## Conclusions

Additional work is needed to better understand the relationships of the chaetodontids, particularly among the species-rich subgenera of *Chaetodon*. Webb (1998), Webb and Blum (1990), Webb and Smith (2000), and the present study have examined the morphology of the laterophysic connection in 22 of 87 species in all *Chaetodon* subgenera except *Roaops*. Clearly, the next step will be to examine the morphology of the laterophysic connection in additional *Chaetodon* species, particularly in the subgenus *Roaops*, which has been difficult because of its deep-water habitat and rarity in museum collections. This study found that the *Chaetodon* subgenus *Chaetodon* (sensu Blum, 1988) showed intrasubgeneric variation in the morphology of the laterophysic connection. Because variation was found among the seven species in this subgenus, more species in the species-rich subgenera *Exornator* and *Rabdophorus* need to be examined histologically in order to better characterize the morphology of their laterophysic connections.

Blum (1988, p. 6) argued that “qualitative skeletal evolution has not kept pace with speciation [and]... osteology does not provide the data necessary to estimate relationships within groups of closely related species” of butterflyfishes. Our work has demonstrated that histological studies of soft-tissue anatomy can provide valuable characters to clarify chaetodontid relationships. The type of laterophysic connection found primitively in the genus *Chaetodon* remains unknown because an unambiguous optimization was not possible. Additional species-level phylogenetic analyses, particularly among the speciose *Chaetodon* subgenera may help resolve this ambiguity. Finally, DNA sequence data should be added to help resolve relationships among these morphologically similar species. McMillan and Palumbi (1995, 1997) and McMillan et al. (1999) analyzed DNA sequence data from the mitochondrial d-loop in 15 *Chaetodon* species. Their analysis, in combination with behavioral and morphological studies, resulted in the synonymy of two species (*C. pelewensis* and *C. punctatofasciatus*); future studies combining molecular, morphological, and behavioral characters should be able to provide the evidence necessary to provide a species-level phylogeny for this important percoid family.

## Acknowledgments

We thank those who collected fishes for us and who provided access to specimens in their care: B. Brown and M. Stiassny (AMNH); K. Hartel (MCZ); J. Leis and M. McGrouther (AMS); C. Meyer (University of Hawaii); D. Daget and W. Saul (ANSP); and B. DuVall and R. Fournier (New Jersey State Aquarium). We would

like to thank N. Cicchino, N. Kelly, S. Ky, G. Seavy, and M. Turnipseed who assisted in the preparation of histological material. We thank L. Ferry-Graham (UC Davis) for providing access to page proofs prior to the publication of her group’s work on the evolution of long jaws in butterflyfishes. Finally, we thank the following individuals for discussions, reading this paper, and/or offering numerous and valuable suggestions for its improvement: K. Smith (Columbia University); J. Faivovich, T. Grant, R. Schelly, S. Schaefer, J. Sparks, M. Stiassny, K. Tang (AMNH); M. Russell, A. Bauer (Villanova University). A special thanks is given to C. Ferraris (formerly of CAS) for his short course in zoological nomenclature that helped resolve the availability and authorship of the *Chaetodon* subgenus *Tetragonopterus*. This work was supported by the Department of Biology at Villanova University, an American Museum of Natural History Lerner-Grey Fellowship to W.L.S., and NSF Grant IBN-9603896 to J.F.W.

## Appendix A

Material examined (species identification, descriptive information [when present], collection site [when known], gender [when known], standard length [in mm]).

*Histological material examined* (specimens sectioned transversely unless otherwise noted).

*Chaetodontidae*: 1. *Chaetodon aureofasciatus* (Cq1 [formerly AMS 24678030], 57.0). 2. *Chaetodon auriga* (Ca2, aquarium trade, 61.0). 3. *Chaetodon baronessa* (Cb1 [formerly AMS 21915011], 55.0). 4. *Chaetodon capistratus* (Cc1, aquarium trade, 25.0; Cc2, aquarium trade, 52.0; Cc4, aquarium trade, female, 49.0). 5. *Chaetodon ephippium*, (Ce1, aquarium trade, 51.0). 6. *Chaetodon kleinii* (uncat, aquarium trade, 70.0; Ck10, Oahu, Hawaii, male, 85.0; Ck11, Oahu, Hawaii, female, 81.0; Ck13, Oahu, Hawaii, female, 74.0). 7. *Chaetodon meyeri* (Cy1, aquarium trade, 85.0). 8. *Chaetodon miliaris* (Cr1, Oahu, Hawaii, 100.0; Cr4, Oahu, Hawaii, 56.0; Cr9, Oahu, Hawaii, 50.0; Cr11, Oahu, Hawaii, 45.0). 9. *Chaetodon multicinctus* (Cm4, Oahu, Hawaii, male, 87.0; Cm5, Oahu, Hawaii, female, 90.0; Cm7, Oahu, Hawaii, male, 90.0; Cm9, Oahu, Hawaii, female, 83.0). 10. *Chaetodon ocellatus* (MCZ 76604, tholichthys postlarva, 7.0; Cl6, Tuckerton, New Jersey, tholichthys postlarva, 17.4; Cl7, Tuckerton, New Jersey, 41.8). 11. *Chaetodon octofasciatus* (uncat., aquarium trade, 50.0; Co9, Oahu, Hawaii, female, 73.0; Co11, Oahu, Hawaii, female, 63.0; Co12, Oahu, Hawaii, female, 67.0; Co14, Oahu, Hawaii, male, 77.0; Co20, aquarium trade, male, 73.0; Co22, aquarium trade, horiz. section, female, 58.0; Co30, aquarium trade, male, 64.0). 12. *Chaetodon oligacanthus* (Cg1 [formerly ANSP 100113], 67.0). 13. *Chaetodon ornaticinctus* (Cn1, aquarium trade, female, 68.0; Cn4, aquarium trade, 61.0). 14. *Chaetodon plebeius* (Cp1



## Appendix C

Characters examined in the phylogenetic analyses. The “B” followed by a number, when present, refers to the character number used in Blum (1988). Additive characters are followed by [A], the non-additive character is followed by [N], and uninformative/autapomorphic characters are followed by [U].

1. (B1). Dorsal pterygiophore [see Blum (1988, Figs. 13–17)]: pterygiophore simple; first dorsal spine buttressed ventrally by lateral processes of the pterygiophore (derived from state 0) = 1; pterygiophore with lateral processes anterior to erector dorsalis (derived from state 1) = 2; pterygiophore with lateral processes (fused early in ontogeny <20 mm) surrounding erector dorsalis (derived from state 2) = 3. [additive binary coded, A, CI = 1.0, RI = 1.0]. This character was coded as an additive binary character forming multiple transformation series as hypothesized by Blum (1988, pp. 111–112).
2. (B2). Supraneurals [see Blum (1988, Figs. 13–18)]: no sequential articulation between first dorsal pterygiophores, supraneurals, and supraoccipital crest = 0; sequential articulation between supraoccipital, supraneurals, and first dorsal pterygiophore = 1; first dorsal pterygiophore flattened and lacking posterior groove for second supraneural = 2; single supraneural present (indicative of fusion) = 3; heads of supraneurals thickened, but first retains postero-dorsal groove = 4 [additive binary coded, A, CI = 1.0, RI = 1.0]. Because two of the five character states were coded as unknown in *Chaetodon oligacanthus*, this character was coded as an additive binary character allowing all available information to be coded.
3. (B3). Pleural ribs extending almost to mid ventral [see Blum (1988, Figs. 11 and 12)]: no = 0; yes = 1 [U, CI = 1.0, RI = 1.0].
4. (B4). Pleural rib laminae [see Blum (1988, Figs. 11 and 12)]: without anterior laminae = 0; with weakly developed anterior laminae = 1; with well-developed anterior laminae = 2 [A, CI = 0.67, RI = 0.5].
5. (B5). Basipterygio-postcleithral ligament present [see Blum (1988, Fig. 12)]: no = 0; yes = 1 [U, CI = 1.0, RI = 1.0].
6. (B6). Lateral line: not truncate = 0; truncate = 1 [CI = 1.0, RI = 1.0].
7. (B7). Lateral line scales: less than 60 = 0; more than 60 = 1 [CI = 0.5–1.0, RI = 0.0–1.0].
8. Swim bladder horns: absent = 0; present = 1 [CI = 1.0, RI = 1.0].
9. (B9). Swim bladder constriction: absent = 0; present = 1 [CI = 1.0, RI = 1.0].
10. (B10). Kidney morphology: posterior kidney not extending beyond first hemal spine = 0; posterior kidney with bilateral lobes = 1; bilateral lobes fused around first hemal spine = 2 [A, CI = 0.67, RI = 0.75].
11. (B11). Anterior two branchiostegal rays free from ceratohyal [see Blum (1988, Figs. 20 and 21)]: no = 0; yes = 1 [U, CI = 1.0, RI = 1.0].
12. (B12). Branchiostegal rays reduced to five: no = 0; yes = 1 [CI = 0.5, RI = 0.75].
13. (B13). Basihyal large and robust with prominent ventral keel [see Blum (1988, Figs. 20 and 21)]: no, rod shaped = 0; yes = 1 [CI = 0.5–1.0, RI = 0.85–1.0].
14. (B14). Hyoid artery foramen present in dorsal hypohyal: yes = 0; no = 1 [CI = 0.5, RI = 0.9].
15. (B15). Dorsal hypohyal flattened and swept posteriorly [see Blum (1988, Figs. 20 and 21)]: no = 0; yes = 1 [CI = 1.0, RI = 1.0].
16. (B16). First epibranchial shape in anterior view [see Blum (1988, Fig. 23)]: longer than high = 0; the height and width equal, the axis inclined medially, the dorsal cartilage is wide and protrudes above the dorsal margin, and the lateral cartilage is relatively tall = 1; the height to width ratio is 0.75, the axis inclined medially, and all of the cartilages are relatively small, particularly the dorsal and lateral ones = 2; the height and width are roughly equal, the axis is horizontal, the medial cartilage is small, and the dorsal and lateral cartilages are wide and tall = 3; the height to width ratio is slightly less than one, the axis is declined medially, the medial cartilage is larger than in all other taxa, and the dorsal and lateral cartilages are of moderate size = 4 [N, CI = 1.0, RI = 1.0].
17. (B17). Third basibranchial and hypobranchial are broad and flat [see Blum (1988, Fig. 24)]: yes = 0; no, not flattened, but narrow and rod-like = 1 [CI = 0.5–1.0, RI = 0.0–1.0].
18. (B18). Jaw and tooth morphology [see Blum (1988, Figs. 25–27)]: pomacanthid morphology = 0; five to ten teeth rows are positioned such that there is generally an overlap of teeth rows within each band (derived from state 0) = 1; five bands of teeth, tooth arrangement disorganized, short curved jaw teeth (derived from state 1) = 2; vertical orientation of now shortened teeth, more than three bands of teeth rows (derived from state 2) = 3; jaw teeth short and straight, only two bands (derived from state 1) = 4; jaw teeth straight and long, rows short, reduced overlap of rows (derived from state 1) = 5; all teeth on the descending premaxillary process absent (derived from state 5) = 6; teeth of nearly equivalent length, coalesced into brush with increased number of bands (derived from state 6) = 7 [additive binary coded, A, CI = 0.78–0.89, RI = 0.86–0.92]. This character

- was coded as an additive binary character forming multiple transformation series as hypothesized by Blum (1988).
19. (B19). Vomerine teeth: well-developed patch = 0; partially toothed = 1; toothless = 2 [A, CI = 0.22, RI = 0.63].
  20. (B20). Ethmoid foramen completely enclosed in the lateral ethmoid: yes = 0; no, medial margin of foramen is formed by the mesethmoid = 1 [CI = 1.0, RI = 1.0].
  21. (B21). Bone quality composing posterior face of the mesethmoid: posterior face of mesethmoid solid = 0; posterior face of mesethmoid perforated by numerous small holes = 1; posterior face of mesethmoid covered with more holes such that the holes comprise a greater total area than the bone = 2 [A, CI = 0.33, RI = 0.77].
  22. (B22). Position of posterior mesethmoid: beyond lateral ethmoids = 0; between lateral ethmoids = 1 [CI = 0.25–0.33, RI = 0.4–0.6].
  23. (B23). Two vertical ridges present on the anterior mesethmoid, lateral to the premaxillary fenestra: no = 0; yes = 1 [CI = 0.5, RI = 0.88].
  24. (B24). Ethmomaxillary ligament present: yes = 0; no = 1 [CI = 0.33, RI = 0.60].
  25. Palato-palatine ligament (ppl) [see Blum (1988, Figs. 29–33)]: originates on medial face of palatine's maxillary process = 0; moved postero-dorsally, some fibers originating from apophysis = 1 [CI = 1.0, RI = 1.0].
  26. Apophysis on palatine's maxillary process under ppl [see Blum (1988, Figs. 29–33)]: no apophysis = 0; small apophysis = 1; large apophysis = 2 [additive binary coded, A, CI = 0.67, RI = 0.92]. Because one of the three character states was coded as missing in *Chaetodon oligacanthus*, this character was coded as an additive binary character allowing all available information to be coded.
  27. (B27). Basal section of the palatine is dorsoventrally narrow and rod-like: no, roughly triangular in sagittal view = 0; yes = 1 [CI = 0.5–1.0, RI = 0.5–1.0].
  28. (B28). Ectopterygoid wide [see Blum (1988, Figs. 29–34)]: no, flat and boomerang shaped with one arm directed ventrally and the other directed antero-dorsally = 0; yes, ventral arm broad = 1. [CI = 0.33, RI = 0.5].
  29. (B29). Second circumorbital excluded from margin of orbit: no = 0; yes = 1 [CI = 1.0, RI = 1.0].
  30. (B30). Third circumorbital with ventrally directed lamina: no = 0; yes = 1 [CI = 0.33–0.5, RI = 0.33–0.66].
  31. (B31). Parietal reduced dorsoventrally [see Blum (1988, Figs. 35 and 36)]: no, only anteroposterior reduction of the parietal = 0; yes, the parietal remains in contact with the supraoccipital dorsally, but loses its ventral contact with the pterotic. = 1 [CI = 1.0, RI = 1.0].
  32. (B32). Lateral extrascapular not enclosing temporal canal [see Blum (1988, Fig. 37)]: no, all three sensory canals are enclosed in the lateral extrascapular = 0; yes, the temporal canal and the junction of all three canals are exposed laterally = 1 [CI = 1.0, RI = 1.0].
  33. (B33). Medial extrascapular disc-like: no, simple and tubular = 0; yes = 1 [CI = 1.0, RI = 1.0].
  34. Palato-vomerine ligaments: outgroup condition = 0; separated = 1; on maxillary process = 2 [A] [CI = 1.0, RI = 1.0].
  35. Vertical palato-vomerine ligament on palatine apophysis: absent = 0; present = 1 [CI = 0.33, RI = 0.77].
  36. Laterophysic connection type: indirect = 0; direct = 1 [CI = 0.33, RI = 0.50].
  37. Swim bladder-peritoneal relationship: attached = 0; free = 1 [CI = 0.33, RI = 0.60].
  38. Swim bladder horn width (see text): comparatively wide = 0; very narrow = 1 [CI = 1.0, RI = 1.0].
  39. Swim bladder horn length: reaches supracleithral lateral line canal (SLLC) = 0; does not reach SLLC = 1 [U, CI = 1.0, RI = 1.0].
  40. Mucoid connective tissue deep to supracleithral lateral-line canal: absent = 0; present = 1 [CI = 0.25, RI = 0.25].
  41. Supracleithral lateral-line canal: medially complete or enclosed = 0; medially incomplete or exposed = 1 [CI = 1.0, RI = 1.0].

#### Appendix D

Classification of chaetodontid species recognized in this study by Allen et al. (1998), Maugé and Bauchot (1984), and Nalbant (1971, 1973, 1986, 1991, 1995). Taxon names listed under authors are the supraspecific categories into which each species was placed. All species maintained their specific epithet in all taxonomies except for our *Chaetodon (Megaprotodon) oligacanthus*, which was recognized as *Parachaetodon ocellatus* in all three other classifications. The term “unrecognized” is used for species that were not listed by the authors or were not considered valid by these authors. Supraspecific names marked with an “#” under Allen et al. are taxa that were recognized by these authors, but not placed into subgenera in their classification on pp. 240–242; their subgeneric classification was based on information elsewhere in their text. Taxa examined histologically are in bold type, and taxa that were examined (cleared and stained, radiographed, or alcoholic specimens) by Blum (1988) or in the present study are followed by “\*.” The type species for each supraspecific taxon is underlined.

## Appendix D (continued)

Species	Allen et al.	Maugé and Bauchot	Nalbant
<i>Amphichaetodon howensis</i> *	<i>Amphichaetodon</i>	<i>Johnrandallia</i>	<i>Amphichaetodon</i>
<i>Amphichaetodon melbae</i> *	<i>Amphichaetodon</i>	<i>Johnrandallia</i>	<i>Amphichaetodon</i>
<i>Chelmon marginalis</i> *	<i>Chelmon</i>	<i>Chelmon</i>	<i>Chelmon</i>
<i>Chelmon muelleri</i> *	<i>Chelmon</i>	<i>Chelmon</i>	<i>Chelmon</i>
<i>Chelmon rostratus</i> *	<i>Chelmon</i>	<i>Chelmon</i>	<i>Chelmon</i>
<i>Chelmonops curiosus</i>	<i>Chelmonops</i>	Unrecognized	Unrecognized
<i>Chelmonops truncatus</i> *	<i>Chelmonops</i>	<i>Chelmonops</i>	<i>Chelmonops</i>
<i>Coradion altivelis</i> *	<i>Coradion</i>	<i>Coradion</i>	<i>Coradion</i>
<i>Coradion chrysozonus</i> *	<i>Coradion</i>	<i>Coradion</i>	<i>Coradion</i>
<i>Coradion melanopus</i>	<i>Coradion</i>	<i>Coradion</i>	<i>Coradion</i>
<b><i>Forcipiger flavissimus</i>*</b>	<i>Forcipiger</i>	<i>Forcipiger</i>	<i>Forcipiger</i>
<i>Forcipiger longirostris</i>	<i>Forcipiger</i>	<i>Forcipiger</i>	<i>Forcipiger</i>
<i>Hemitaurichthys multispinosus</i>	<i>Hemitaurichthys</i>	<i>Hemitaurichthys Acanthotaurichthys</i>	<i>Acanthotaurichthys</i>
<i>Hemitaurichthys polylepis</i> *	<i>Hemitaurichthys</i>	<i>Hemitaurichthys Hemitaurichthys</i>	<i>Hemitaurichthys</i>
<i>Hemitaurichthys thompsoni</i> *	<i>Hemitaurichthys</i>	<i>Hemitaurichthys Hemitaurichthys</i>	Nox
<i>Hemitaurichthys zoster</i>	<i>Hemitaurichthys</i>	<i>Hemitaurichthys Hemitaurichthys</i>	<i>Hemitaurichthys</i>
<i>Heniochus acuminatus</i>	<i>Heniochus</i>	<i>Heniochus</i>	<i>Heniochus</i>
<i>Heniochus chrysostomus</i> *	<i>Heniochus</i>	<i>Heniochus</i>	<i>Heniochus</i>
<i>Heniochus diphreutes</i> *	<i>Heniochus</i>	Unrecognized	Unrecognized
<i>Heniochus intermedius</i> *	<i>Heniochus</i>	<i>Heniochus</i>	<i>Heniochus</i>
<i>Heniochus monoceros</i>	<i>Heniochus</i>	<i>Heniochus</i>	<i>Heniochus</i>
<i>Heniochus pleurotaenia</i>	<i>Heniochus</i>	<i>Heniochus</i>	<i>Heniochus</i>
<i>Heniochus singularius</i>	<i>Heniochus</i>	<i>Heniochus</i>	<i>Heniochus</i>
<i>Heniochus varius</i> *	<i>Heniochus</i>	<i>Heniochus</i>	<i>Heniochus</i>
<i>Johnrandallia nigrirostris</i> *	<i>Johnrandallia</i>	<i>Johnrandallia</i>	<i>Johnrandallia</i>
<i>Roa excelsa</i> *	<i>Chaetodon Roa</i>	<i>Chaetodon Roa</i>	<i>Chaetodon Paracanthochaetodon</i>
<i>Roa jayakari</i>	<i>Chaetodon Roa</i> #	<i>Chaetodon Roa</i>	<i>Chaetodon Paracanthochaetodon</i>
<i>Roa modestus</i>	<i>Chaetodon Roa</i>	<i>Chaetodon Roa</i>	<i>Roa</i>
<i>Prognathodes aculeatus</i>	<i>Prognathodes</i>	<i>Prognathodes Prognathodes</i>	<i>Prognathodes</i>
<i>Prognathodes aya</i> *	<i>Prognathodes</i>	<i>Prognathodes Prognathodes</i>	<i>Bauchotia</i>
<i>Prognathodes brasiliensis</i>	Undescribed	Undescribed	Undescribed
<i>Prognathodes carlhubbsi</i>	Unrecognized	Undescribed	<i>Prognathodes Bauchotia</i>
<i>Prognathodes dichrous</i>	<i>Prognathodes</i>	<i>Prognathodes</i>	<i>Prognathodes Bauchotia</i>
<i>Prognathodes falcifer</i>	<i>Prognathodes</i>	<i>Prognathodes</i>	<i>Prognathodes Bauchotia</i>
<i>Prognathodes guezai</i>	<i>Prognathodes</i>	<i>Prognathodes</i>	Unrecognized
<i>Prognathodes guyanensis</i>	<i>Prognathodes</i>	<i>Prognathodes</i>	<i>Prognathodes Bauchotia</i>
<i>Prognathodes guyotensis</i> *	<i>Prognathodes</i>	Unrecognized	<i>Peterscotia</i>



<i>Prognathodes marcellae</i>	<i>Prognathodes</i>	<i>Prognathodes</i>	<i>Prognathodes Bauchotia</i>
<i>Prognathodes obliquus</i>	<i>Prognathodes</i>	Unrecognized	<i>Prognathodes Bauchotia</i>
<b><i>Chaetodon striatus*</i></b>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Chaetodon</i>
<b><i>Chaetodon (Chaetodon) capistratus*</i></b>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Chaetodon</i>
<i>Chaetodon (Chaetodon) hoefleri*</i>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Roa</i>	<i>Chaetodon Chaetodon</i>
<i>Chaetodon (Chaetodon) humeralis</i>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Roa</i>	<i>Chaetodon Chaetodon</i>
<i>Chaetodon (Chaetodon) marleyi</i>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Byssochaetodon</i>	<i>Chaetodon Chaetodon</i>
<b><i>Chaetodon (Chaetodon) ocellatus*</i></b>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Chaetodon</i>
<i>Chaetodon (Chaetodon) robustus</i>	<i>Chaetodon Chaetodon</i>	<i>Chaetodon Byssochaetodon</i>	<i>Chaetodon Lepidochaetodon</i>
<i>Chaetodon (Rabdophorus) adiergastos*</i>	<i>Chaetodon Chaetodontops</i>	<i>Chaetodontops</i>	<i>Chaetodon Chaetodontops</i>
<b><i>Chaetodon (Rabdophorus) auriga*</i></b>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Linophora</i>	<i>Chaetodon Linophora</i>
<i>Chaetodon (Rabdophorus) auripes</i>	<i>Chaetodon Chaetodontops</i>	<i>Chaetodontops</i>	<i>Chaetodon Chaetodontops</i>
<i>Chaetodon (Rabdophorus) collare*</i>	<i>Chaetodon Chaetodontops</i>	<i>Chaetodontops</i>	<i>Chaetodon Chaetodontops</i>
<i>Chaetodon (Rabdophorus) decussatus</i>	<i>Chaetodon Rabdophorus</i>	Incertae sedis (Chaetodontidae)	Unrecognized
<i>Chaetodon (Rabdophorus) dialeucos</i>	<i>Chaetodon Chaetodon</i>	Undescribed	Undescribed
<b><i>Chaetodon (Rabdophorus) ephippium*</i></b>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Rabdophorus</i>	<i>Chaetodon Rabdophorus</i>
<i>Chaetodon (Rabdophorus) falcata*</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Oxychaetodon</i>	<i>Chaetodon Oxychaetodon</i>
<i>Chaetodon (Rabdophorus) fasciatus*</i>	<i>Chaetodon Chaetodontops</i>	<i>Rabdophorus Linophora</i>	<i>Chaetodon Chaetodontops</i>
<i>Chaetodon (Rabdophorus) flavirostris*</i>	<i>Chaetodon Chaetodontops</i>	<i>Chaetodontops</i>	<i>Chaetodon Chaetodontops</i>
<i>Chaetodon (Rabdophorus) gardineri*</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Aspilurochaetodon</i>	Unrecognized
<i>Chaetodon (Rabdophorus) leucopleura</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Aspilurochaetodon</i>	<i>Chaetodon Rabdophorus</i>
<i>Chaetodon (Rabdophorus) lineolatus*</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Oxychaetodon</i>	<i>Chaetodon Oxychaetodon</i>
<i>Chaetodon (Rabdophorus) lunula*</i>	<i>Chaetodon Chaetodontops</i>	<i>Chaetodontops</i>	<i>Chaetodon Chaetodontops</i>
<i>Chaetodon (Rabdophorus) melannotus*</i>	<i>Chaetodon Chaetodon</i>	<i>Mesochaetodon Strongylochaetodon</i>	<i>Chaetodon Chaetodontops</i>
<i>Chaetodon (Rabdophorus) mesoleucos*</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Oxychaetodon</i>	<i>Chaetodon Oxychaetodon</i>
<i>Chaetodon (Rabdophorus) nigropunctatus*</i>	<i>Chaetodon Rabdophorus</i>	<i>Chaetodon Apporetochaetodon</i>	<i>Chaetodon Chaetodontops</i>
<i>Chaetodon (Rabdophorus) ocellicaudus*</i>	<i>Chaetodon Chaetodon</i>	<i>Mesochaetodon Strongylochaetodon</i>	Unrecognized
<i>Chaetodon (Rabdophorus) oxycephalus</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Oxychaetodon</i>	<i>Chaetodon Oxychaetodon</i>
<i>Chaetodon (Rabdophorus) pictus</i>	Unrecognized	Unrecognized	<i>Chaetodon Linophora</i>
<i>Chaetodon (Rabdophorus) rafflesi*</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Linophora</i>	<i>Chaetodon Linophora</i>
<i>Chaetodon (Rabdophorus) selene*</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Aspilurochaetodon</i>	<i>Chaetodon Linophora</i>
<i>Chaetodon (Rabdophorus) semeion*</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Rabdophorus</i>	<i>Chaetodon Rabdophorus</i>
<b><i>Chaetodon (Rabdophorus) semilarvatus*</i></b>	<i>Chaetodon Chaetodontops</i>	<i>Chaetodontops</i>	<i>Chaetodon Oxychaetodon</i>
<i>Chaetodon (Rabdophorus) ulietensis*</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Oxychaetodon</i>	<i>Chaetodon Oxychaetodon</i>
<i>Chaetodon (Rabdophorus) vagabundus*</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Linophora</i>	<i>Chaetodon Linophora</i>
<i>Chaetodon (Rabdophorus) wiebeli*</i>	<i>Chaetodon Chaetodontops</i>	<i>Chaetodontops</i>	<i>Chaetodon Chaetodontops</i>
<i>Chaetodon (Rabdophorus) xanthocephalus</i>	<i>Chaetodon Rabdophorus</i>	<i>Rabdophorus Rabdophorus</i>	<i>Chaetodon Rabdophorus</i>
<i>Chaetodon (Exornator) argentatus*</i>	<i>Chaetodon Rhombochaetodon</i>	<i>Exornator Rhombochaetodon</i>	Incertae sedis (Chaetodontidae)
<i>Chaetodon (Exornator) assarius</i>	<i>Chaetodon Chaetodon</i>	<i>Heterochaetodon Heterochaetodon</i>	<i>Chaetodon Exornator</i>
<i>Chaetodon (Exornator) blackburnii*</i>	<i>Chaetodon Chaetodon</i>	<i>Megaprotodon</i>	Incertae sedis (Chaetodontidae)
<i>Chaetodon (Exornator) citrinellus*</i>	<i>Chaetodon Chaetodon</i>	<i>Exornator Exornator</i>	<i>Chaetodon Exornator</i>

## Appendix D (continued)

Species	Allen et al.	Maugé and Bauchot	Nalbant
<i>Chaetodon (Exornator) daedalma</i> *	<i>Chaetodon Chaetodon</i>	<i>Exornator Exornator</i>	<i>Chaetodon Lepidochaetodon</i>
<i>Chaetodon (Exornator) dolosus</i> *	<i>Chaetodon Chaetodon</i>	<i>Heterochaetodon Heterochaetodon</i>	Unrecognized
<i>Chaetodon (Exornator) fremblii</i> *	<i>Chaetodon Chaetodon</i>	<i>Heterochaetodon Lepidochaetodon</i>	Incertae sedis (Chaetodontidae)
<i>Chaetodon (Exornator) guentheri</i> *	<i>Chaetodon Chaetodon</i>	<i>Exornator Exornator</i>	<i>Chaetodon Exornator</i>
<i>Chaetodon (Exornator) guttatissimus</i> *	<i>Chaetodon Chaetodon</i>	<i>Exornator Exornator</i>	<i>Chaetodon Exornator</i>
<i>Chaetodon (Exornator) litus</i>	<i>Chaetodon Chaetodon</i>	<i>Heterochaetodon Burgessius</i>	Unrecognized
<i>Chaetodon (Exornator) madagascariensis</i> *	Unrecognized	<i>Exornator Rhombochaetodon</i>	Incertae sedis (Chaetodontidae)
<i>Chaetodon (Exornator) mertensii</i> *	<i>Chaetodon Rhombochaetodon</i>	<i>Exornator Rhombochaetodon</i>	Incertae sedis (Chaetodontidae)
<b><i>Chaetodon (Exornator) miliaris</i>*</b>	<i>Chaetodon Chaetodon</i>	<i>Heterochaetodon Burgessius</i>	<i>Chaetodon Exornator</i>
<b><i>Chaetodon (Exornator) multinctus</i>*</b>	<i>Chaetodon Chaetodon</i>	<i>Exornator Exornator</i>	<i>Chaetodon Exornator</i>
<i>Chaetodon (Exornator) paucifasciatus</i> *	<i>Chaetodon Rhombochaetodon</i>	<i>Exornator Rhombochaetodon</i>	Incertae sedis (Chaetodontidae)
<b><i>Chaetodon (Exornator) punctatofasciatus</i>*</b>	<i>Chaetodon Chaetodon</i>	<i>Exornator Exornator</i>	<i>Chaetodon Exornator</i>
<i>Chaetodon (Exornator) quadrimaculatus</i> *	<i>Chaetodon Chaetodon</i>	<i>Heterochaetodon Lepidochaetodon</i>	<i>Chaetodon Tifia</i>
<i>Chaetodon (Exornator) sanctaehelena</i> *	<i>Chaetodon Chaetodon</i>	<i>Heterochaetodon Heterochaetodon</i>	Unrecognized
<b><i>Chaetodon (Exornator) sedentarius</i></b>	<i>Chaetodon Chaetodon</i>	<i>Heterochaetodon Heterochaetodon</i>	Unrecognized
<i>Chaetodon (Exornator) smithi</i>	<i>Chaetodon Chaetodon</i>	<i>Heterochaetodon Burgessius</i>	Unrecognized
<i>Chaetodon (Exornator) xanthurus</i> *	<i>Chaetodon Rhombochaetodon</i>	<i>Exornator Rhombochaetodon</i>	Incertae sedis (Chaetodontidae)
<i>Chaetodon (Roaops) burgessi</i> *	<i>Chaetodon Roa</i>	<i>Roaops</i>	<i>Roaops</i>
<i>Chaetodon (Roaops) declivis</i>	<i>Chaetodon Roa</i>	<i>Roaops</i>	<i>Roaops</i>
<i>Chaetodon (Roaops) flavocoronatus</i>	<i>Chaetodon Roa</i>	Unrecognized	<i>Roaops</i>
<i>Chaetodon (Roaops) mitratus</i>	<i>Chaetodon Roa</i>	<i>Roaops</i>	<i>Roaops</i>
<i>Chaetodon (Roaops) nippon</i> *	<i>Chaetodon Roa</i>	<i>Mesochaetodon Mesochaetodon</i>	<i>Chaetodon Lepidochaetodon</i>
<i>Chaetodon (Roaops) tinkeri</i> *	<i>Chaetodon Roa</i>	<i>Roaops</i>	<i>Roaops</i>
<i>Chaetodon (Lepidochaetodon) interruptus</i>	<i>Chaetodon Lepidochaetodon</i> #	Unrecognized	<i>Chaetodon Lepidochaetodon</i>
<b><i>Chaetodon (Lepidochaetodon) kleinii</i>*</b>	<i>Chaetodon Chaetodon</i>	<i>Exornator Exornator</i>	<i>Chaetodon Lepidochaetodon</i>
<i>Chaetodon (Lepidochaetodon) trichrous</i> *	<i>Chaetodon Chaetodon</i>	<i>Mesochaetodon Mesochaetodon</i>	Unrecognized
<b><i>Chaetodon (Lepidochaetodon) unimaculatus</i>*</b>	<i>Chaetodon Lepidochaetodon</i>	<i>Heterochaetodon Lepidochaetodon</i>	<i>Chaetodon Lepidochaetodon</i>
<b><i>Chaetodon (Megaprotodon) trifascialis</i>*</b>	<i>Chaetodon Megaprotodon</i>	<i>Megaprotodon</i>	<i>Chaetodon Megaprotodon</i>
<b><i>Chaetodon (Megaprotodon) oligacanthus</i>*</b>	<i>Parachaetodon ocellatus</i>	<i>Parachaetodon ocellatus</i>	<i>Parachaetodon ocellatus</i>
<i>Chaetodon (Tetrachaetodon) andamanensis</i>	Undescribed	Undescribed	Undescribed
<i>Chaetodon (Tetrachaetodon) bennetti</i> *	<i>Chaetodon Tetrachaetodon</i>	<i>Nalbantius</i>	<i>Chaetodon Tetrachaetodon</i>
<b><i>Chaetodon (Tetrachaetodon) plebeius</i>*</b>	<i>Chaetodon Tetrachaetodon</i>	<i>Megaprotodon</i>	<i>Chaetodon Tetrachaetodon</i>
<i>Chaetodon (Tetrachaetodon) speculum</i> *	<i>Chaetodon Tetrachaetodon</i>	<i>Nalbantius</i>	<i>Chaetodon Tetrachaetodon</i>
<i>Chaetodon (Tetrachaetodon) zanzibariensis</i> *	<i>Chaetodon Tetrachaetodon</i>	<i>Nalbantius</i>	Unrecognized



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