

Phylogeny of the Chaetodontids on the Basis of Kidney and Intestinal Differentiations

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(Received September 4, 1980)

Abstract The chaetodontid kidneys and intestinal coiling patterns were classified. Morphological variations of these systems were analyzed to elucidate the chaetodontid phylogenies. The present data suggest that (1) all chaetodontids (not including pomacanthids, *Microcanthus*, and *Vinculum*) share a common ancestor; (2) except for *Forcipiger*, *Hemitaurichthys*, *Heniochus*, and *Johnrandallia*, the rest of the chaetodontids form a monophyletic group; (3) *Chelmon* and *Chelmonops* are closely related groups; (4) within the monophyletic group including *Chaetodon* and *Parachaetodon*, *Parachaetodon*, *Prognathodes* series of the genus *Chaetodon*, and some *Chaetodon* species are more closely related to each other than to other *Chaetodon* species; (5) the similarity in kidney morphology among *Forcipiger*, *Hemitaurichthys*, *Heniochus*, and *Johnrandallia* provides no strong evidence for their monophyly. The proposed chaetodontid phylogeny was compared to previously hypothesized phylogenies.

According to recent literature, the butterflyfishes and angelfishes have been recognized as separate families, namely, the Chaetodontidae and Pomacanthidae, respectively. In the present study we adopt this classification for practical reasons.

The chaetodontid butterflyfishes have received much study in the past. Many proposals regarding the classification and phylogenetic interrelationships of the chaetodontid genera and species have been made. Ahl (1923) included eleven genera (*Chaetodon*, *Chelmon*, *Chelmonops*, *Coradion*, *Forcipiger*, *Hemitaurichthys*, *Heniochus*, *Microcanthus*, *Parachaetodon*, *Prognathodes*, and *Vinculum*) in this group. Fraser-Brunner (1945) removed the genus *Microcanthus* and placed it in the family Scorpidae. Burgess (1978) made the same change with *Vinculum*. While studying the eastern Pacific chaetodontids and their Atlantic relatives, Hubbs and Rehnitz (1958) discussed the phylogenetic position of *Chaetodon nigrrostris*. They concluded that *C. nigrrostris* should be referred to the genus *Heniochus* rather than *Chaetodon* principally because of its complete lateral line. Nalbant (1971, 1973, 1974) classified all chaetodontid species (approximately 120 species) into ten genera, ninety species in *Chaetodon*, nine in *Prognathodes*, seven in *Heniochus*, with the remaining seven genera, *Chelmon*, *Chelmonops*,

Coradion, *Forcipiger*, *Hemitaurichthys*, *Parachaetodon*, and *Johnrandallia*, including one to three species each. *Johnrandallia* was erected by Nalbant in his 1974 paper. This is a monotypic genus and the type species is *Sarothrodus nigrrostris* Gill which has often been included in *Chaetodon*. Burgess (1978) described two genera, *Amphichaetodon* and *Pseudochaetodon*. The former genus includes two species. The type species of *Pseudochaetodon* is *Sarothrodus nigrrostris* Gill. *Johnrandallia* is a senior synonym of *Pseudochaetodon*. The limitation of the genus *Chaetodon* is unsettled. Unlike most workers (e.g., Hubbs and Rehnitz, 1958), Burgess (1978) reduced the genus *Prognathodes* to a subgenus within *Chaetodon* where he placed ninety species. The monophyly of *Chaetodon* in Burgess's classification (including *Prognathodes* series) remains to be tested. The reduced lateral line has been treated as the sole derived character diagnostic of this genus (e.g., Burgess, 1978). However, this character state of the lateral line is not unique to *Chaetodon* spp. but is also shared by *Parachaetodon*, a monotypic genus. Therefore, no synapomorphic character is present only in *Chaetodon*. Hubbs and Rehnitz (1958) strongly favored the phylogenetic significance of the lateral line character in chaetodontids. However, the phylogenetic interrelationships of *Parachaetodon ocellatus* and

other *Chaetodon* species are unknown at the present time. Burgess recognized a related problem and said, "It is assumed that a reduced lateral line occurred only once, but if this cannot be confirmed, and if there are indications that a reduced lateral line occurred more than once, then some subgenera of *Chaetodon* might have to be elevated to genera, and some realignment of genera would necessarily occur." (Burgess, 1978: 106).

The above proposals were supported by evidence from comparative studies on the morphological variation of the following structures or characters: lateral line, dorsal spine sheath, dorsal and anal spine and ray counts, dorsal spine length, dorsal fin shape, body form, snout length, head length, neurocranium appearance, caudal and dorsal fin skeletons, and body color pattern. Thorough comparative studies of osteological, myological, nervous, excretory, and digestive systems are limited. Study of these latter systems should provide a better understanding of the phylogeny of these fishes.

The complex intestinal coiling patterns of acanthurids and zancrids provide evidence of their phylogenetic relationships (Mok, 1977). The highly diverse kidney morphology of the centrarchids (Mok, 1978) also provide indices for phylogenetic relationships. The long intestine of most chaetodontids within the small volume of their body cavity generally results in complex intestinal coiling patterns. These complex patterns are more phylogenetically informative than a simple one (Mok, 1978). The complex intestinal patterns of some chaetodontids from Taiwan and their implications to phylogenetic study of the chaetodontids were investigated by Shen and Lam (1979). Chaetodontid kidneys also show various structural forms. They therefore offer some promise for progress in the study of systematics of this group. The objective of this study are to: 1) classify chaetodontid kidney forms and intestinal coiling patterns, 2) survey the distribution of these types in chaetodontids, 3) interpret the interrelationships of the recognizable patterns, 4) propose theory (or theories) of chaetodontid generic or specific phylogenies on the basis of kidney and intestinal coiling morphologies, 5) compare these theories with the prevailing ideas of chaetodontid phylogenies.

Materials and methods

Specimens examined in this study were from the fish collection of the American Museum of Natural History (AMNH), Australian Museum, Sydney (AMS), Academy of Natural Sciences of Philadelphia (ANSP), California Academy of Sciences (CAS), Department of Biological Sciences, Florida Atlantic University (FAU), Harbor Branch Foundation, Inc. (HBF), the Museum of the Department of Zoology, National Taiwan University (NTUM), South Australian Museum (SAM), U.S. National Museum (USNM), and Western Australian Museum (WAM).

The intestinal tract was removed and its gross morphology was drawn under the dissecting microscope. The intestinal coiling pattern was converted from the drawing of the intestinal tract by tracing the latter with a continuous line. These patterns are shown in the left side view. The kidney was easily observed after swimbladder removal and described according to Mok (1978).

Twenty-six species of the chaetodontids and twenty-seven species of other perciforms were examined (numbers in parentheses are catalogue numbers and standard length measurements in millimeters):

Chaetodontids: *Amphichaetodon howensis* (AMS I. 17268-002, 52 mm; AMS I. 17412-001, 94 mm; AMS I. 17365-002, 123 mm), *Chaetodon aculeatus* (AMNH 34556, 60 mm), *C. argentatus* (NTUM uncat. 53 mm, 64 mm, 73 mm), *C. auriga* (AMNH 33605, 145 mm, NTUM uncat., 58 mm), *C. aya* (AMNH 13740, 87 mm; HBF 107: 5009, 70 mm, 90 mm), *C. capistratus* (AMNH 21279, 19 mm; AMNH 26299, 31 mm; AMNH 37144, 74 mm; FAU-73-15, 11 mm, 21 mm, 23 mm, 25 mm; FAU-EXII-68-8, 50 mm, 50 mm), *C. lunula* (NTUM uncat., 103 mm), *C. modestus* (NTUM uncat. 97 mm), *C. ocellatus* (AMNH 28537, 21 mm, 37 mm; AMNH 17054, 110 mm; FAU uncat., 52 mm), *C. plebeius* (FAU-74-41, 51 mm; NTUM 00618, 85 mm), *C. sedentarius* (AMNH 29115, 27 mm; AMNH 19032, 77 mm, 80 mm; FAU uncat., 33 mm), *C. striatus* (AMNH 21220, 20 mm; AMNH 36698, 55 mm; AMNH 997, 80 mm; FAU uncat., 33 mm, 35 mm, 52 mm), *C. triangulum* (NTUM uncat., 40 mm), *C. unimaculatus* (NTUM uncat., 60 mm, 97 mm, 107 mm), *C.*

vagabundus (AMNH 14790, 58 mm; FAU-74-41, 57 mm), *Chelmon rostratus* (AMNH 16665, 90 mm; CAS 37641, 94 mm; NTUM uncat., 81 mm), *Chelmonops truncatus* (WAM P13745, 131 mm), *Coradion altivelis* (AMS I. 17122-001, 75 mm; AMS I. 15658-023, 85 mm; AMS IB. 7667, 90 mm), *C. chrysozonus* (AMNH 18390, 85 mm; NTUM uncat., 110 mm, 141 mm, 142 mm), *Forcipiger flavissimus* (NTUM uncat., 94 mm, 127 mm, 130 mm), *Hemitaurichthys poly-lepis* (AMNH uncat., 91 mm, 132 mm; NTUM uncat., 70 mm, 76 mm, 122 mm, 134 mm), *Heniochus acuminatus* (NTUM uncat., 45 mm, 51 mm, 78 mm), *H. chrysostomus* (NTUM uncat., 40 mm, 41 mm, 42 mm, 45 mm, 46 mm, 46 mm), *H. monoceros* (NTUM uncat., 75 mm, 101 mm), *H. singularis* (NTUM uncat., 42 mm, 81 mm), *H. varius* (NTUM uncat., 50 mm, 52 mm, 77 mm), *Johnrandallia nigrirostris* (CAS 14018, 105 mm; CAS 45214, 47 mm), *Parachaetodon ocellatus* (WAM P25095-019, 83 mm).

Non-chaetodontid periciforms: Cichlidae (*Cichlasoma champotonis* AMNH 24527, 72 mm; *C. heterospilum* AMNH 25102, 69 mm; *C. salvini* AMNH 35008, 72 mm; *Haplochromis eucinostomus* AMNH 31855, 78 mm), Enoplosidae (*Enoplosus armatus* AMS I. 7178-007, 95 mm), Ephippidae (*Chaetodipterus faber* USNM 188288, 80 mm; *Platax* sp. AMNH uncat. 42 mm, 84 mm), Kyphosidae (*Girella melanichthys* NTUM uncat., 46 mm; *G. mezzina* AMNH 26935, 108 mm; *Kyphosus sectatris* AMNH uncat., 230 mm; *K. vaigiensis* AMNH 14804, 135 mm; *Sector ocyurus* AMNH 12659, 28 mm; *Atypichthys strigatus* AMS E. 1785, 124 mm; AMS I. 15912-013, 41 mm, 45 mm, 67 mm, 76 mm, 78 mm; *Microcanthus strigatus* AMNH 33608, 87 mm; NTUM uncat., 123 mm; *Neatypus obliquus* WAM P4640, 128 mm, 150 mm, 154 mm; WAM P5105, 110 mm, 111 mm, 116 mm; WAM P13735, 122 mm; *Scorpius aequipinnis* AMNH 31314, 63 mm; *S. georgianus* AMNH 31315, 77 mm; *Vinculum sexfasciatus* SAM F1291, 177 mm), Labridae (*Bodianus rufus* AMNH 34004, 90 mm), Odacidae (*Odax pullus* ANSP 113340, 63 mm), Pentacerotidae (*Histioporus typus* AMNH uncat. 133 mm), Pomacanthidae (*Centropyge bicolor* AMNH uncat., 55 mm; *Holacanthus tricolor* AMNH 28703, 70 mm; *Pomacanthus paru* AMNH 30340, 62 mm), Scatophagidae (*Selenotoca multifasciata* AMNH 33645, 74 mm;

Scatophagus argus AMNH 15878, 63 mm; NTUM uncat., 60 mm), Sciaenidae (*Aplodinotus grunniens* AMNH uncat., 145 mm).

Results

Classification of chaetodontid kidney types

Type 1. The left and right posterior kidneys fuse anteriorly to the base (or the proximal end) of the first haemal spine; kidney tissue from this fused portion of the kidney extends posteriorly on both sides of the first haemal spine; the distal ends of these posterior kidney extensions may reach the first interhaemal spine but they do not fuse medially (Fig. 1B). Type 1 occurs in *Forcipiger* (e.g., *F. flavissimus*), *Hemitaurichthys* (e.g., *H. polylepis*), *Heniochus* (e.g., *H. acuminatus*, *H. chrysostomus*, *H. varius*), and *Johnrandallia* (*J. nigrirostris*).

Type 2. This type resembles Type 1 except that the distal ends of the posterior kidney extensions fuse medially at the rear tip of the

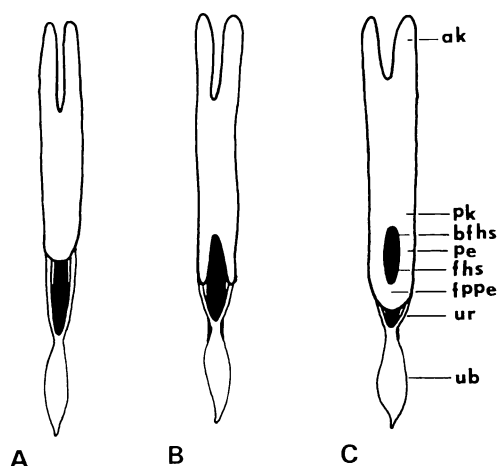


Fig. 1. Ventral views of (A) the generalized periciform kidney, (B) a Type-1 chaetodontid kidney, and (C) a Type-2 chaetodontid kidney. ak, anterior kidney; bfhs, base (or proximal end) of the first haemal spine; fhs, first haemal spine (also indicated by the upper portion of the black column); fppe, fused portion of the posterior extensions of the posterior kidney; pe, posterior extension of the posterior kidney; pk, posterior kidney; ub, urinary bladder; ur, ureter. The lower portion of the black column near the urinary bladder represents the first interhaemal spine.

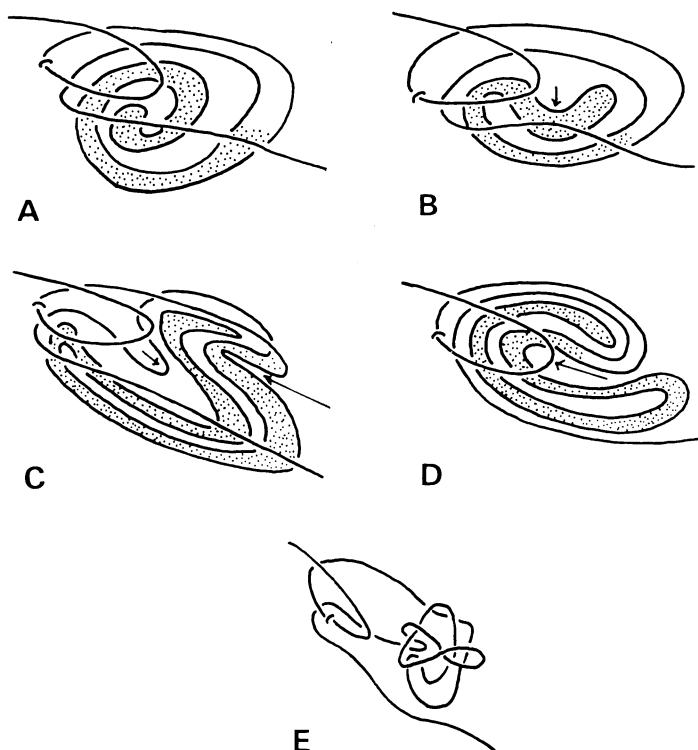


Fig. 2. Left side views of the five chaetodontid intestinal coiling patterns. A: Type 1. B: Type 2. C: Type 3. D: Type 4. E: Type 5. —(—, Junction between the stomach and the intestine; stippling, loop a; short arrow, downward or backward folding at the rear section of loop a; longer arrow, forward folding at the anterior section of loop a.

swimbladder (Fig. 1C). Type 2 occurs in *Amphichaetodon* (e.g., *A. howensis*), *Chaetodon* (e.g., *C. aculeatus*, *C. argentatus*, *C. auriga*, *C. aya*, *C. ocellatus*, *C. plebeius*, *C. sedentarius*, *C. unimaculatus*, *C. vagabundus*; some authors used the name *Prognathodes aculeatus* and *P. aya* for the first and fourth species; e.g., Hubbs and Rechnitzer, 1958; Nalbant, 1971), *Chelmon* (e.g., *C. rostratus*), *Chelmonops* (*C. truncatus*), *Coradion* (e.g., *C. altivelis*, *C. chrysozonus*), and *Para-chaetodon* (*P. ocellatus*).

Kidneys of some non-chaetodontid perciforms

Scatophagus argus, *Selenotoca multifasciata* (Scatophagidae), *Girella melanichthys*, *G. meina*, *Kyphosus sectatris*, *K. vaigiensis*, *Sectator ocyurus*, *Atypichthys strigatus*, *Neotypus obliquus* (110 mm, 111 mm, 116 mm, 122 mm, 128 mm, 150 mm), *Microcanthus strigatus* (87 mm), *Scorpius georgianus*, *Vinculum sexfasciatus* (Kyphosidae), and *Enoplosus armatus* (Enoplosidae) have the gen-

eralized perciform kidney type in which the left and right kidneys fuse anteriorly to the base (or the proximal end) of the first haemal spine; no kidney tissue extends posteriorly beyond this point (Mok, 1978; Fig. 1A). *Scorpius aequipinnis* (Kyphosidae) has a Type-1 kidney and *Histiopertus typus* (Pentacerotidae) has a Type-2 kidney. Other possible chaetodontid relatives such as pomacanthids (e.g., *Centropyge bicolor*, *Holacanthus tricolor*, *Pomacanthus paru*), ephippids (*Platax* sp.) also possess the generalized perciform kidney type. *Chaetodipterus faber* (Ephippidae), however, has a Type-2 kidney. Besides *Scorpius aequipinnis* (Kyphosidae), Type 1 only appears in *Cichlasoma champotonis*, *C. heterospilum*, *C. salvini*, *Haplochromis eucinostomus* (Cichlidae), *Aplodinotus grunniens* (Sci-aenidae), *Bodianus rufus* (Labridae). Type 2 appears in *Odax pullus* (Odacidae) in addition to its presence in *Histiopertus typus* and *Chaetodipterus faber*.

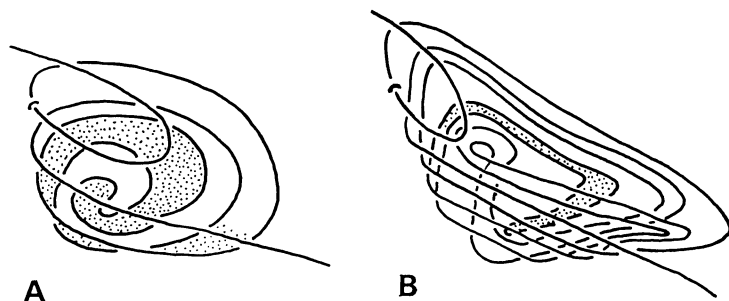


Fig. 3. Left side views of two Type-1 intestinal coiling patterns. A: *Chaetodon modestus* (97 mm). B: *Chaetodon unimaculatus* (107 mm). -(-, Junction of the stomach and intestine; stippling, loop a.

Ontogenetic change of chaetodontid kidney morphology

In *Chaetodon capistratus* a 11-mm specimen has a Type-1 kidney whereas a 21-mm and a 50-mm specimen have a Type-2 kidney.

Classification of chaetodontid intestinal coiling patterns

Type 1. The major long loop on the right (or behind) of the rectum (or loop a; Mok, 1977, 1978, 1980) winds in a strictly dextral fashion forming a spiral intestinal mass (Fig. 2A). This type only occurs in a few species of *Chaetodon* (e.g., *Chaetodon modestus* and *C. unimaculatus*; Fig. 3A, B, respectively).

Type 2. Loop a winds dextrally; the rear section of this loop folds downward or backward (or rightward) (Fig. 2B; arrow indicates this folding direction). This type appears in *Para-chaetodon* (*P. ocellatus*) and it is common in *Chaetodon* (e.g., *C. aculeatus*, *C. aya*, *C. argenteatus*, and *C. triangulum*; Fig. 4). The patterns of *C. bennetti* (105 mm SL) and *C. trifascialis* (103 mm), which were reported but not described in detail by Shen and Lam (1979), are autapomorphic forms derived from a Type-2 pattern (Fig. 5A, C, respectively). In *C. bennetti*, the downward folding at the rear end of loop a develops into a forward (or leftward) folding, an uncommon condition (Fig. 5B; short arrow indicates this folding). Due to the increasing length of loop a, a backward (or rightward) folding appears at the mid section of this loop (long arrow in Fig. 5B). In *C. trifascialis* a counter-clockwise folding develops at the mid section of loop a (long arrow in Fig. 5D) and the downward folding at the rear end of loop a is also present (short arrow in Fig. 5D).

Type 3. Loop a winds dextrally; the rear section of this loop folds backward (or rightward) (Fig. 2C; short arrow indicates this backward folding); the anterior section of loop a folds forward (or leftward) (Fig. 2C; long arrow indicates this forward folding). This type appears only in *Chaetodon* but is common within this genus. Numerous *Chaetodon* species among those examined have this type: *C. auriga*, *C. capistratus*, *C. lunula*, *C. ocellatus*, *C. plebeius*, and *C. vagabundus* (Fig. 6).

Type 4. Loop a winds dextrally; the anterior section of loop a folds forward (or leftward) (Fig. 2D; long arrow indicates this folding); the downward or backward folding at the rear section of loop a is absent. This type is limited to *Chelmon* and *Chelmonops* (Fig. 7B, C, respectively).

Type 5. Loop a is not well defined in this type. The coiling direction of the intestine does not clearly follow an orderly dextral pathway. Fig. 2E gives an example of this type. The pattern of *Amphichaetodon* (e.g., *A. howensis*), *Coradion* (e.g., *C. altivelis*, *C. chrysozonus*), *Forcipiger* (e.g., *F. flavissimus*), *Hemitaenichthys* (e.g., *H. polylepis*), *Heniochus* (e.g., *H. acuminatus*, *H. chrysostomus*, *H. monoceros*, *H. singularis*, and *H. varius*), and *Johnrandallia* (*J. nigrirostris*) fit the definition of the Type-5 pattern. Due to the broad definition of Type-5 and the significant species-specific variation, detailed descriptions of their patterns are given below.

Amphichaetodon. The gut of only one out of the three specimens of *Amphichaetodon howensis* available is not damaged. This 52-mm specimen has a simpler intestinal coiling pattern in comparison with the 123-mm specimen in which the gut is partly damaged. The tip of loop

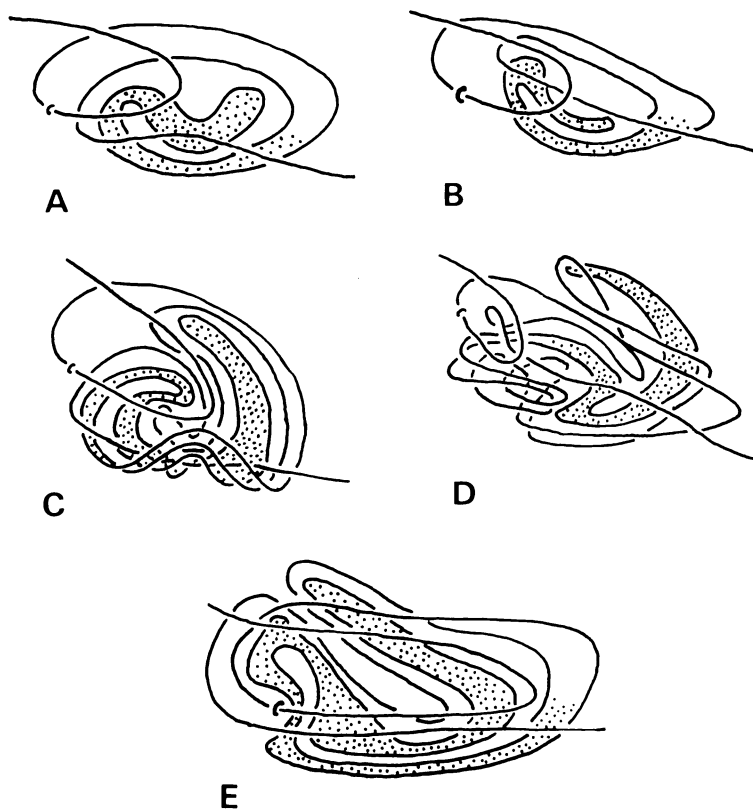


Fig. 4. The Type-2 patterns of five chaetodontids. A: *Chaetodon aculeatus* (60 mm). B: *C. aya* (87 mm). C: *C. argentatus* (73 mm). D: *C. triangulum* (40 mm). E: *Parachaetodon ocellatus* (83 mm).

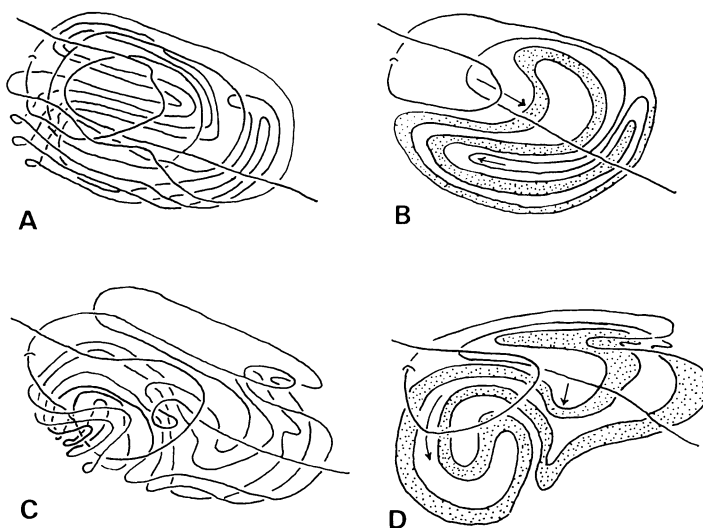


Fig. 5. Intestinal coiling patterns of (A) *Chaetodon bennetti* (105 mm), (B) *C. bennetti* (105 mm; simplified pattern), (C) *C. trifascialis* (103 mm), and (D) *C. trifascialis* (103 mm; simplified pattern). Arrows point to particular sections of the intestinal patterns, see text for detail. (After Shen and Lam, 1979).

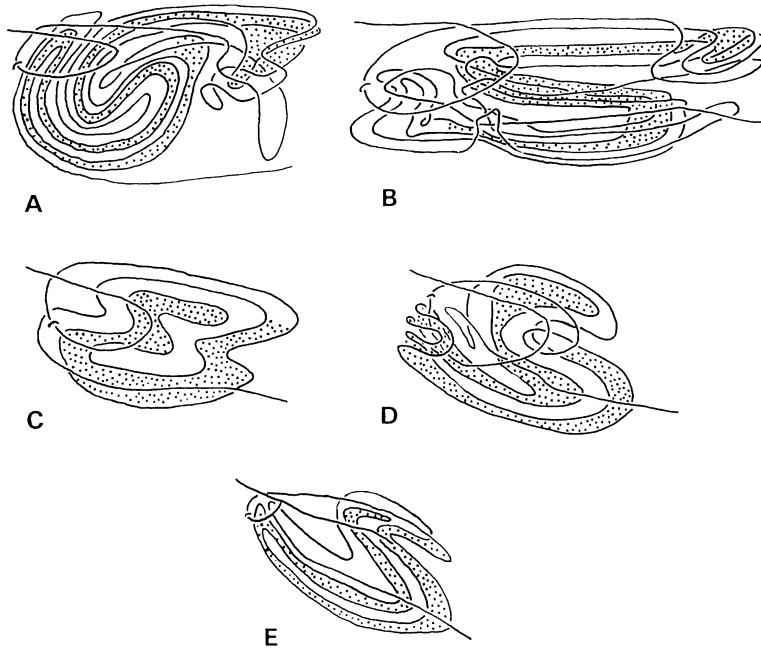


Fig. 6. The Type-3 intestinal coiling patterns of five *Chaetodon* species. A: *Chaetodon auriga* (145 mm). B: *C. capistratus* (74 mm). C: *C. lunula* (103 mm). D: *C. plebeius* (85 mm). E: *C. vagabundus* (58 mm).

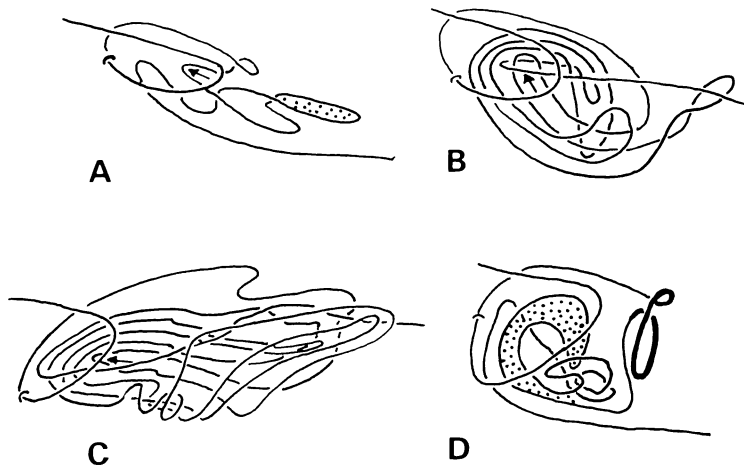


Fig. 7. The intestinal coiling patterns of (A) *Amphichaetodon howensis* (52 mm), (B) *Chelmon rostratus* (90 mm), (C) *Chelmonops truncatus* (131 mm), and (D) *Johnrandallia nigrirostris* (47 mm).

a in the former specimen is recognizable (Fig. 7A; stippled area represents loop **a**). A forward folding appears at the anterior section of the intestine (arrow in Fig. 7A indicates this folding). In spite of the resemblance among the forward (or leftward) foldings in this 52-mm specimen of *A. howensis*, *Chelmon*, and *Chel-*

monops, we do not intend to support the homology of these foldings at this point. We feel that individual variation of the *A. howensis* pattern may be fairly high. Examinations made on more specimens of *A. howensis* and *A. melbae* are necessary before we can define the generic characteristics of the *Amphichaetodon* intestinal

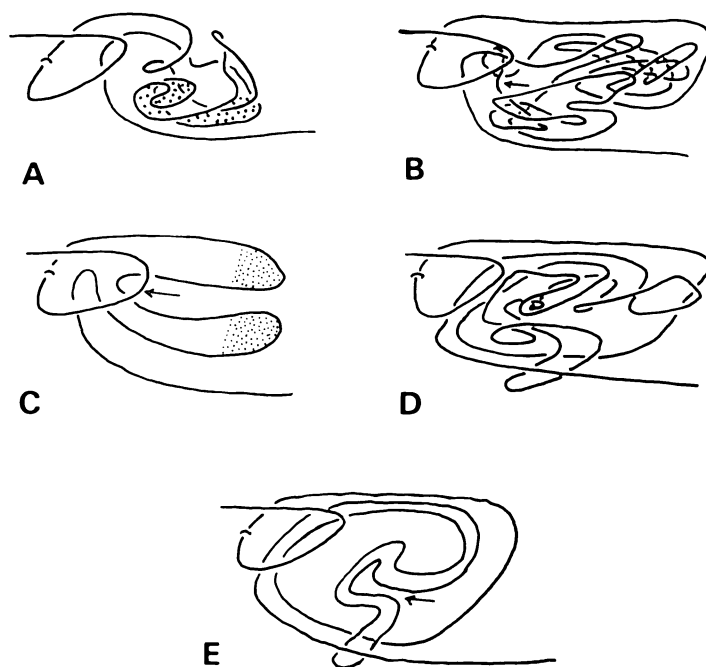


Fig. 8. The intestinal coiling patterns of (A) *Coradion altivelis* (75 mm), (B) *C. altivelis* (85 mm), (C) a Type-HZ pattern, (D) *C. altivelis* (90 mm), and (E) *C. altivelis* (90 mm; simplified pattern). Arrow, forward (or leftward) folding of the intestine; heavy stippling, loop a; fine stippling, loops found in a Type-HZ pattern.

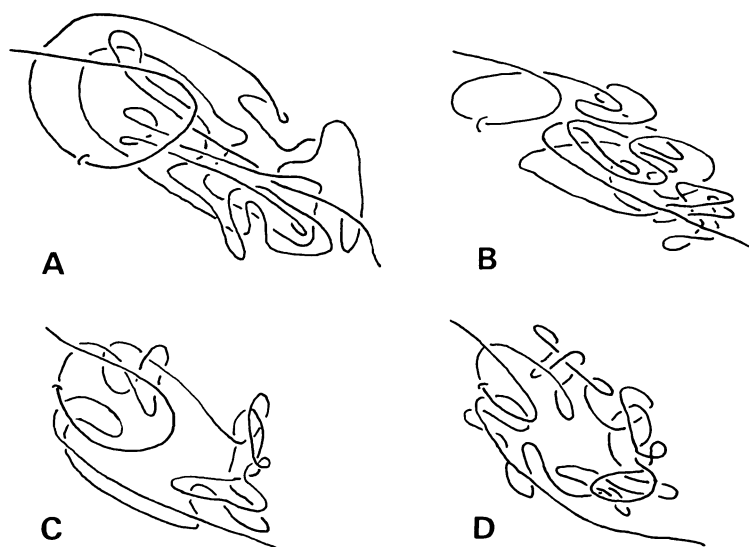


Fig. 9. The intestinal coiling patterns of *Coradion chryzozonus*. A: 85 mm. B: 110 mm. C: 141 mm. D: 142 mm.

coiling pattern. Unfortunately, these specimens are not available to us at the present time.

Coradion. Specimens of *Coradion altivelis*

and *C. chryzozonus* were studied. In the former species, the patterns of the 75-, 85- and 90-mm specimens are different. Loop a of the 75-mm

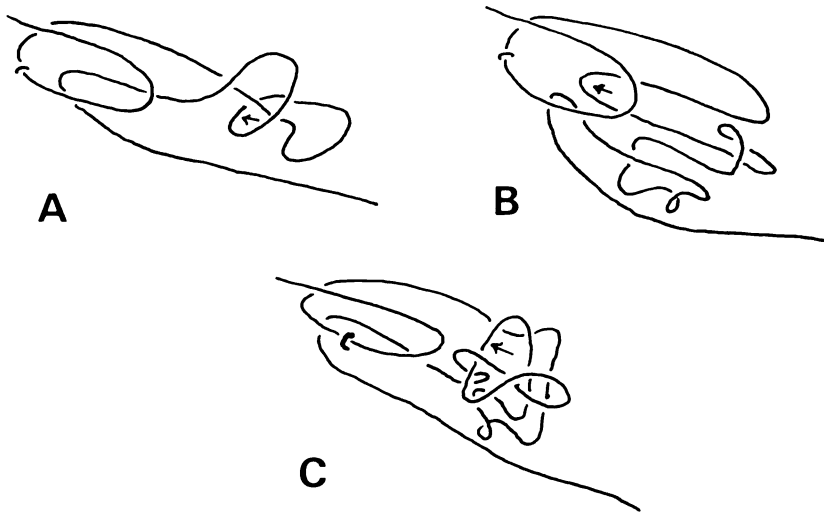


Fig. 10. The intestinal coiling patterns of *Forcipiger flavissimus*. A: 94 mm. B: 127 mm. C: 130 mm. Arrow, forward (or leftward) folding of the intestine.

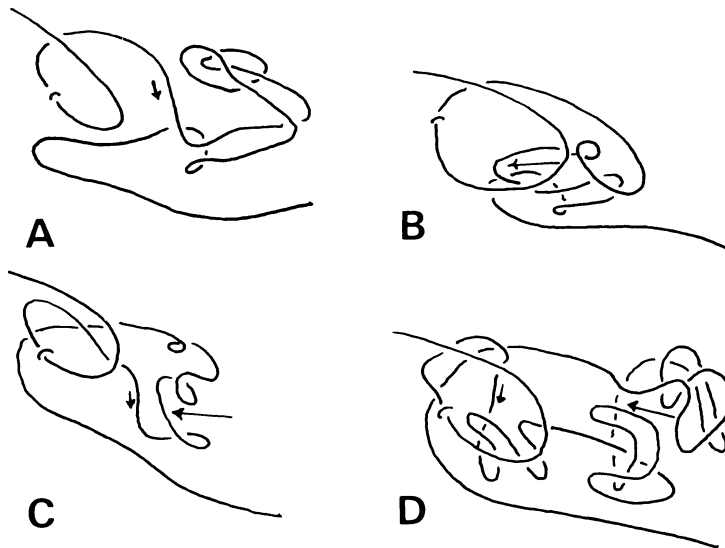


Fig. 11. The intestinal coiling patterns of *Hemitaenichthys polylepis*. A: 91 mm. B: 71 mm. C: 122 mm. D: 134 mm. Long arrow, forward (or leftward) folding of the intestine; short arrow, sharp bending at the anterior section of the intestine.

specimen coils dextrally (Fig. 8A; stippled area represents loop a). In the 85-mm specimen (Fig. 8B) the pattern is considered to be derived from a Type-HZ pattern described by Mok (1980). The tip of loop a in a Type-HZ pattern folds horizontally to the left side (or forward; Fig. 8B, C; short arrow shows this folding) forming two loops (Fig. 8C; fine stipplings re-

present these two loops). Further coilings in these two loops give rise to the pattern of this 85-mm specimen. The intestine of the 90-mm specimen coils in a spiral pathway (Fig. 8D, E) with a forward folding at its mid section (arrow in Fig. 8E points to this folding). In *C. chrysozonus*, the patterns of the 141- and 142-mm specimens are similar; it has a lot of small coil-

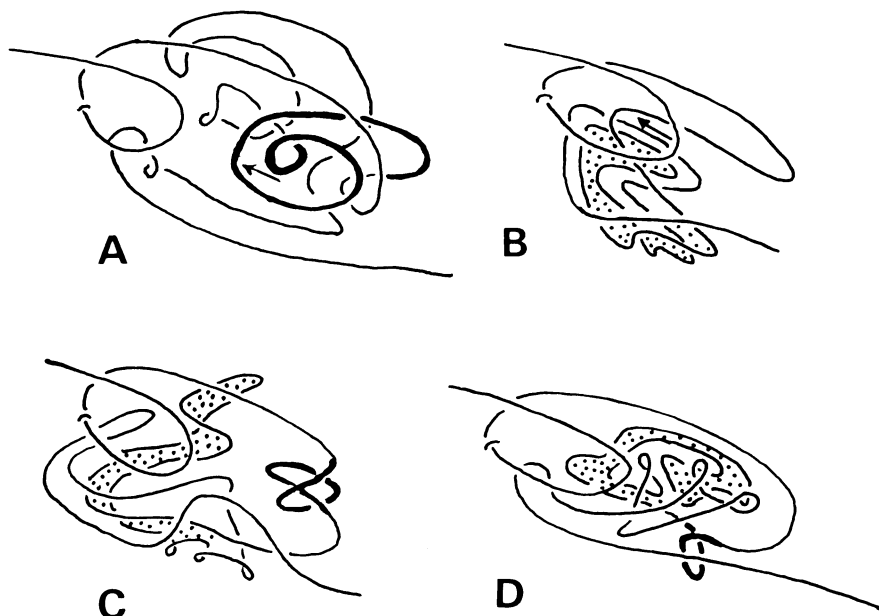


Fig. 12. The intestinal coiling patterns of three *Heniochus* species. A: *H. monoceros* (75 mm). B: *H. singularis* (42 mm). C: *H. singularis* (81 mm). D: *H. varius* (52 mm). Arrow, forward (or leftward) folding of the intestine; heavy line, loop s; stippling, loop a.

ings along the intestine (Fig. 9C, D). Loop a of these specimens is not well distinguishable. Their patterns differ from that of the 85- and 110-mm specimens (Fig. 9A, B). Common characteristics in the patterns of these specimens are unrecognizable. The only obvious feature of the present data regarding the *Coradion* pattern is the lack of patterning due to high individual and species-specific variations. More specimens are needed to reveal the species-specific and generic patterns.

Forcipiger. In spite of the considerable individual variation, a forward (or leftward) folding at the anterior section of the intestine is recognizable in the examined specimens of *F. flavissimus* (Fig. 10; arrows indicate this folding direction). This folding is clearly shown in the 127-mm specimen (Fig. 10B). The pattern of *Forcipiger* therefore can be defined by this forward (or leftward) folding which frequently takes place at the tip of loop a.

Hemitaurichthys. In spite of the considerable individual variation in the examined specimens of *H. polylepis*, the pattern can be defined by a forward (or leftward) folding at the tip of loop a (Fig. 11; long arrows indicate this folding direc-

tion); the anterior section of the intestine tends to bend downward sharply (Fig. 11A, C, D; short arrows indicate this downward bending).

Heniochus. In spite of individual and ontogenetic variations, the patterns of *Heniochus* spp. can be defined by a common character with a forward or upward folding at the anterior section of the intestine (Fig. 12~14; long arrows indicate this folding). Loop a may appear in a certain ontogenetic stage. If it does, it coils dextrally (Fig. 12; stippled areas represent loop a). The development of this forward or upward folding was studied by looking into the ontogenetic change of *H. chrysostomus* and *H. acuminatus* intestinal coiling patterns. In the former species a small loop s is located at the anterior part of the intestine of the 41-, 42-mm specimens (Fig. 13A, B; heavy lines represent loop s). It cannot be recognized in the 45-, 46-, 47-mm specimens in which a forward (or leftward) folding takes place at the corresponding position of loop s (Fig. 13C~E; arrows indicate this folding). The dextral loop a is recognizable in the 41-, 42-, 47-mm specimens (Fig. 13A, B, E; stippled areas represent loop a). In *H. acuminatus* a loop homologous to loop s of *H.*

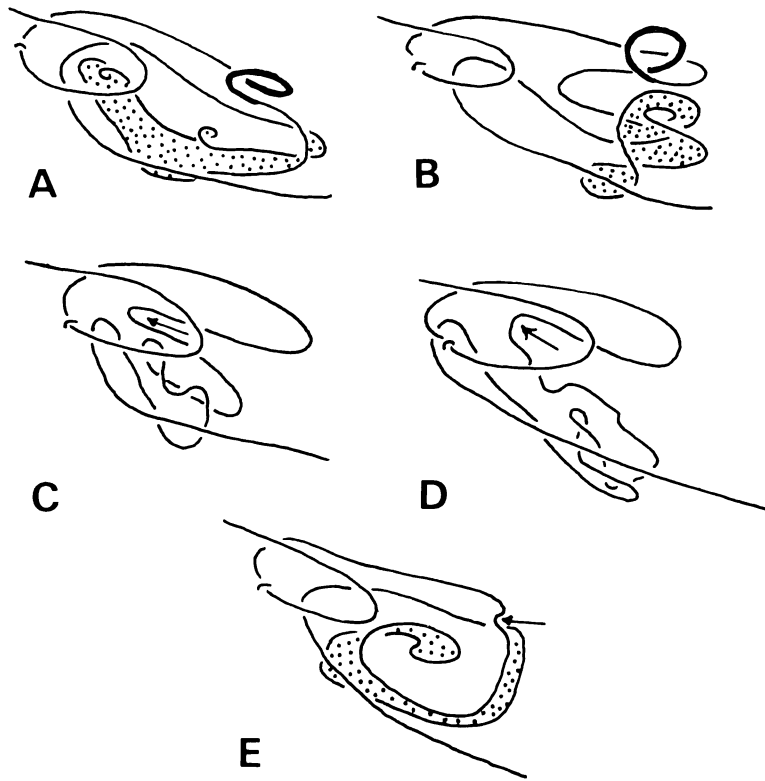


Fig. 13. Ontogenetic variation of the *Heniochus chrysostomus* intestinal coiling patterns. A: 41 mm. B: 42 mm. C: 45 mm. D: 46 mm. E: 47 mm. Arrow, forward (or leftward) folding of the intestine; heavy line, loop s; stippling, loop a.

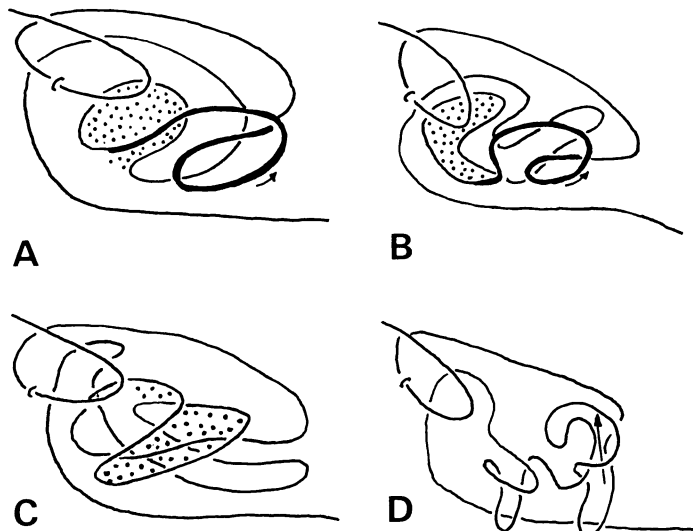


Fig. 14. Ontogenetic change of the *Heniochus acuminatus* intestinal coiling patterns. A: 45 mm. B: 51 mm. C: 51 mm. D: 78 mm. Heavy line, loop s; long arrow, upward folding of the intestine; short arrow, coiling direction of loop s; stippling, loop a.

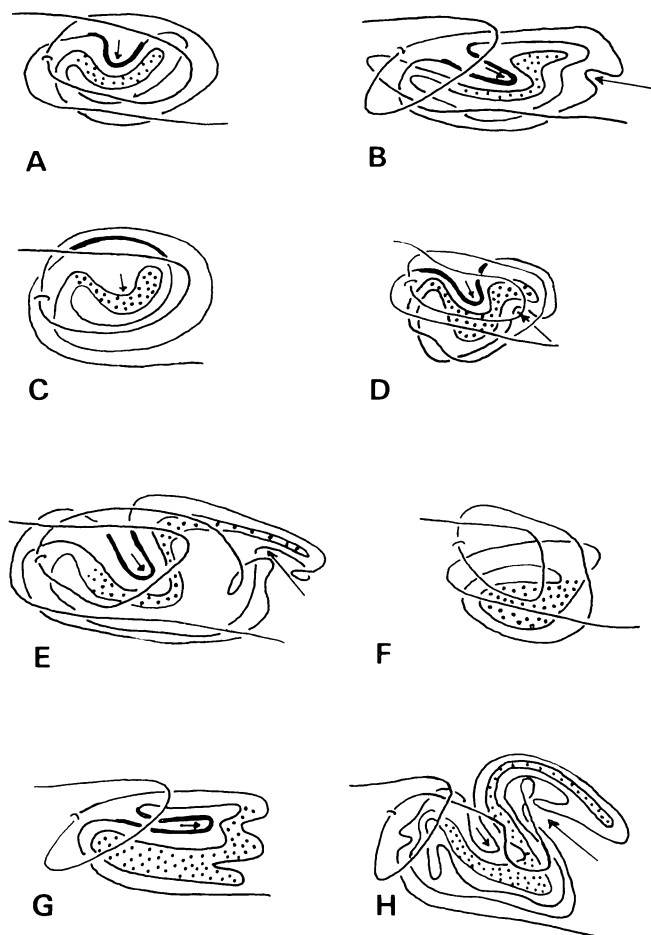


Fig. 15. Ontogenetic change of the intestinal coiling patterns of three *Chaetodon* species. A~B: *C. capistratus* (19 and 31 mm, respectively). C~E: *C. ocellatus* (21, 37 and 110 mm, respectively). F~H: *C. striatus* (20, 55 and 80 mm, respectively). Heavy line, rear section of the intestine; long arrow, forward (or leftward) folding direction of loop a; short arrow, downward or backward folding direction of loop a; stippling, loop a.

chrysostomus is observed (Fig. 14; heavy lines represent this loop). This loop in the 45- and 51-mm specimens looks exactly the same; it is formed by a counter-clockwise coiling process (Fig. 14A, B; short arrows indicate this process). Loop a in these two specimens winds dextrally (Fig. 14A, B; stippled area). Loop s in the other 51-mm specimen is absent (Fig. 14C). In the 78-mm specimen, on the other hand, an upward folding appears (Fig. 14D; long arrow indicates this folding). Loop s is present in *H. monoceros*, *H. singularis*, and *H. varius* (Fig. 12A, C, D; heavy lines represent loop s). This loop is absent in a 42-mm specimen of *H. singularis* (Fig. 12B); it is present, however, in a 81-mm

specimen (Fig. 12C). In the 42-mm specimen a forward (or leftward) folding occurs in the position of loop s instead (Fig. 12B; arrow indicates this folding). We, therefore, hypothesize that loop s and the forward or upward folding in *Heniochus* are homologous characters. In *H. singularis* and *H. varius* loop a coils dextrally (Fig. 12B~D; stippled areas represent this loop).

Johnrandallia. A folding appears at the anterior section of the intestine (Fig. 7D; heavy line indicates this folding); loop a coils dextrally (Fig. 7D; stippled area represents loop a). The location of the former loop is similar to that of loop s in *Heniochus*.

Ontogenetic changes of chaetodontid intestinal patterns

In *Chaetodon capistratus*, *C. ocellatus* and *C. striatus* a Type-2 pattern with the downward or backward folding at the rear end of loop **a** develops earlier than the forward folding at the anterior section of the intestine (Fig. 15). In the former species the downward foldings at the rear section of loop **a** and the rear section of the intestine (indicated by the heavy lines in Fig. 15A, B) develop at approximately the same time. On the other hand, the downward folding of loop **a** in *C. ocellatus* develops earlier than the downward folding at the rear section of the intestine (Fig. 15C, D; heavy lines indicate this section of the intestine). Adult intestinal coiling patterns of these two species are Type 3 (Fig. 15B, E). In *C. striatus* a Type-1 pattern appears in an early ontogenetic stage (Fig. 15F). A backward folding at the rear section of the intestine develops later (short arrow in Fig. 15G). Interestingly, such folding does not involve loop **a** (Fig. 15G; stippling). At this ontogenetic stage, the tip of loop **a**, unlike *C. capistratus* and *C. ocellatus*, points anteriorly. Further dextral growth of loop **a** gives rise to a Type-3 adult pattern with a backward folding at the rear part of loop **a** (Fig. 15H).

Discussion

Interrelationships of the chaetodontid kidney types and its implication to generic phylogeny

With regard to the interrelationship of the chaetodontid kidney types, several hypotheses can be made:

1. The first hypothesis considers that the kidney characterized by the posterior extensions on both sides of the first haemal spine is a derived perciform kidney type and is therefore an apomorphic character uniting all chaetodontids into a monophyletic group.

2. The second hypothesis considers the kidney type of the chaetodontid common ancestor as Type 1. An associated interpretation proposes that Type 2 is the derived form within the Chaetodontidae. As a consequence, the possessors of Type 2 (*Amphichaetodon*, *Chaetodon*, *Chelmon*, *Chelmonops*, *Coradion*, and *Parachaetodon*) are monophyletic.

3. The third hypothesis proposes that the

kidney type of the chaetodontid common ancestor belongs to Type 2. An associated interpretation leads to a hypothesis that Type 1 is a derived form within the Chaetodontidae. As a consequence, the possessors of Type 1 kidney (*Forcipiger*, *Hemitaenichthys*, *Heniochus*, and *Johnrandallia*) are monophyletic.

4. The fourth hypothesis considers the kidney type of the chaetodontid common ancestor as a generalized perciform type in which the fused portion of the posterior kidneys does not extend along the sides of the first haemal spine (Fig. 1A; Ogawa, 1961; Mok, 1978) and Type 1 and Type 2 are derived forms within the Chaetodontidae. Type-1 and Type-2 patterns could be evolved independently from the generalized perciform pattern. In other words, Type-2 pattern was derived from the generalized perciform type without passing the stage of Type-1 kidney. Under this assumption, all chaetodontids can be separated into two monophyletic groups: *Amphichaetodon*-*Chaetodon*-*Chelmon*-*Chelmonops*-*Coradion*-*Parachaetodon*-*Prognathodes* and *Forcipiger*-*Hemitaenichthys*-*Heniochus*-*Johnrandallia*.

However, if we assume that Type-2 kidney was derived from the generalized perciform kidney through a Type-1 stage, only Type-2 kidney can be considered as a chaetodontid apomorphic kidney type. This interpretation leads to a conclusion of the monophyly of *Amphichaetodon*-*Chaetodon*-*Chelmon*-*Chelmonops*-*Parachaetodon*-*Prognathodes*, leaving the phylogenetic positions of *Forcipiger*, *Hemitaenichthys*, *Heniochus*, and *Johnrandallia* unsolved. This last hypothesis is not the most parsimonious one in comparison with the above hypotheses. It involves more morphological changes of the kidney throughout the evolution of Chaetodontidae and is not a favorable hypothesis.

Interpretation on ontogenetic change in kidney morphology in chaetodontids based on the Baer's Law (or the associated Biogenetic Law of Müller-Haeckel; e.g., Balinsky, 1970) and outgroup comparison on the distribution of perciform kidney types in Chaetodontidae and its related families based on the criterion of parsimony (e.g., Nelson, 1970) should falsify many of the above hypotheses. The one which cannot be falsified by the present data is preferable and should be subjected to further tests by separate data sets from other comparative morphological or behavioral

studies.

Ontogenetic change. The ontogenetic change of *Chaetodon capistratus* kidney suggests that Type 2 is derived from Type 1. This conclusion can only falsify hypothesis 3. Although the generalized perciform kidney type has not been noticed at any ontogenetic stage, its presence cannot be rejected until a series of specimens are examined. Under the circumstances, hypothesis 4 should remain to be tested. Specimens of young *Chaetodon sedentarius* (33 mm), *Heniochus chrysostomus* (40 mm) examined have developed their adult kidney form.

Outgroup comparison. Ogawa (1961) classified the external shapes of teleostean kidneys into five types on the basis of the degree of fusion of the left and right kidneys and of the development of specific parts of the kidneys. The characteristics of the butterflyfish kidneys were not mentioned in his paper. Mok (1978) provided additional information on the morphology of teleostean kidneys and classified them into 24 types in which the two types of butterflyfish kidneys were included. Scatophagids, kyphosids (including scorpidids), enoplosids, pentacerotids, and pomacanthids have been considered close relatives of chaetodontids (e.g., Burgess, 1978). Except *Scorpius aequipinnis* which has a Type-1 kidney and *Histiogaster typus* which has a Type-2 kidney, other possible relatives of chaetodontids possess the generalized perciform kidney type. Except the above-mentioned examples, Type-1 kidney only appears in one *Cichlasoma* species (out of the seven representative species), one sciaenid species (out of the twelve representative species), and one labrid species (out of the fifteen representative species) among the 413 perciform species examined by Mok (1978). The limited distribution of these two chaetodontid kidney types in the Perciformes (also see Results) suggests that they are derived kidney forms and they might have evolved independently in various perciforms. Because Type 1 is only present in one of the many kyphosids examined, it is considered here as an autapomorphic character within the family Kyphosidae. A similar argument is also applied to the occurrence of Type 2 in Ehippidae. The appearance of Type 2 in *Histiogaster typus* (Pentacerotidae) and the absence of this type in enoplosids, the close relative of pentacerotids (e.g.,

Burgess, 1978), make it plausible that Type 2 is derived independently in the Pentacerotidae.

Combining the information from outgroup comparison and ontogenetic change, hypotheses 1 and 2 mentioned previously are favorable. Due to the common occurrence of the generalized perciform kidney type in most chaetodontid relatives, it is most parsimonious to assume that the hypothetical common ancestor of chaetodontids had developed a kidney type similar to Type 1. As such, Type 2 is a derived form within Chaetodontidae. The appearance of Type 1 and Type 2 in some chaetodontid relatives and perciforms are here considered to be convergence. In other words, we favor hypotheses 1 and 2. According to these hypotheses, we suggest that all chaetodontids share a synapomorphic perciform kidney character with the fused portion of the posterior kidneys extending on both sides of the first haemal and the first interhaemal spines, and that *Amphi-chaetodon*, *Chaetodon*, *Chelmon*, *Chelmonops*, *Coradion*, and *Parachaetodon* form a monophyletic group. We also must conclude that the interrelationships of *Forcipiger*, *Hemitaurichthys*, *Heniochus*, and *Johnrandallia* cannot be resolved by kidney morphology.

Interrelationships of the chaetodontid intestinal coiling patterns and its implication to chaetodontid phylogeny

Ontogenetic change. The ontogenetic changes of *Chaetodon capistratus* and *C. ocellatus* intestinal coiling patterns (see above) suggest that the growth rate of the dextral loop *a* and the appearance time of the downward foldings at the rear sections of the intestine and loop *a* vary among species. They also indicate that the Type-3 pattern is derived from a Type-2 pattern; the latter pattern is evolved from a Type-1 pattern. According to the Baer's Law, 1) Type 1 appears to be the ancestral chaetodontid pattern, 2) the downward or backward folding of loop *a* shared by Types 2 and 3 should have developed earlier in the chaetodontid phylogeny, 3) the forward folding at the anterior section of loop *a* unique to Type-3 pattern, on the other hand, appears later or after the appearance of the downward folding just discussed in the phylogeny. We propose that the possession of the downward or backward folding at the rear end of loop *a*

and the forward folding at the anterior section of loop **a** are apomorphic characters.

The occurrence of a similar forward folding at the anterior section of loop **a** in *Chelmon* and *Chelmonops* creates a problem regarding the homologous state of these characters. Whether a downward folding similar to that of Types 2 and 3 have occurred in early ontogenetic stages in these two genera remains to be studied. This folding, however, is absent in the adults of these genera. If their juveniles do not develop such foldings, a situation we tend to believe to be true, the forward foldings at the anterior section of loop **a** in these genera and the similar character in the Type-3 pattern are considered to have evolved independently. The Type-4 pattern of *Chelmon* and *Chelmonops* is therefore an apomorphic chaetodontid pattern.

Outgroup comparison. Types 1, 2, 3, and 4 fit the definition of Type SP characterized by its spiral loop **a** described by Mok (1980), although these four patterns differ in their detailed coiling fashions. Type SP is considered a derivative of Type D1 (characterized by its shorter dextral loop **a** in comparison with that of Type SP) also described by Mok (1980). Type D1 is rather common in perciforms (Mok, 1980). The chaetodontid Type-1 pattern has only been found in *Scatophagus argus* (Scatophagidae) out of the other chaetodontid relatives (e.g., pentacerotids, enoplosids, ehippids, kyphosids, and pomacanthids) which either have the generalized perciform pattern (e.g., the Type-D1 pattern) or other autapomorphic patterns. Types 2, 3, and 4 are unique to chaetodontids among percoids (also see Mok, 1980) and are apomorphic characters at various levels in the chaetodontid phylogenetic tree.

Summarizing the data from ontogenetic change and outgroup comparison, we conclude that the ancestral chaetodontid intestinal coiling pattern is Type 1. Type 4 hypothesized as an apomorphic pattern, unites *Chelmon* and *Chelmonops* into a monophyletic group. The ancestral intestinal pattern of the group including *Chaetodon* (including the *Prognathodes* series) and *Parachaetodon* is here hypothesized as Type 1. Within this monophyletic group as supported by the lateral line character, Types 2 and 3 are two apomorphic characters in relation to Type 1. Except those *Chaetodon* spp. with Type-1 pat-

terns, all other *Chaetodon* spp. and *Parachaetodon ocellatus* form a monophyletic group by sharing a pattern with a downward or backward folding at the rear part of loop **a** (a character shared by Types 2 and 3 patterns). Within this latter monophyletic group, all possessors of Type 3 (not including *Parachaetodon ocellatus*) form another monophyletic group. In addition to the six *Chaetodon* spp. listed above which have a Type-3 pattern, Shen and Lam (1979) also observed such pattern in *C. auripes* (98 mm), *C. ehippium* (131 mm), and *C. wiebeli* (46 mm). We are in no position to make further comments about the exact phylogenetic positions of the members in this monophyletic group. Since Type-2 pattern is a plesiomorphic character within the *Chaetodon-Parachaetodon* group, possession of this pattern does not indicate a monophyletic relation. As such, the phylogenetic positions of the *Chaetodon* species with a Type-2 pattern in the *Chaetodon-Parachaetodon* group remain unclear. In addition to *Parachaetodon*, *Chaetodon aculeatus*, *C. aya*, *C. argentatus*, and *C. triangulum*, Shen and Lam (1979) also reported the presence of Type-2 pattern in *C. adiergastos* (121 mm), *C. baronessa* (109 mm), *C. citrinellus* (85 mm), *C. kleinii* (64 mm), *C. nippon* (110 mm), *C. ornatissimus* (130 mm), *C. punctatofasciatus* (68 mm), *C. speculum* (110 mm), *C. trifascialis* (103.4 mm), *C. trifasciatus* (96 mm), *C. ulietensis* (122 mm), and *C. xanthurus* (88 mm).

Type-5 patterns are diverse lineages of the basic chaetodontid intestinal coiling pattern in which loop **a** winds in an orderly dextral pathway. Individual and interspecific variations of the pattern in the genera whose patterns belong to Type 5 are much higher than other chaetodontids with either a Type-1, -2, or -3 pattern. Although there is some resemblance between *Heniochus* and *Johnrandallia* (having a loop- or loop s- at the anterior section of the intestine), *Hemitaurichthys* and *Forcipiger* (having a forward folding at the tip of loop **a**), *Amphichaetodon*, *Chelmon*, and *Chelmonops* (having a forward folding at the anterior section of the intestine), we hesitate to propose the synapomorphies of these resemblances. Accordingly, the interpretation of Shen and Lam (1979) on the synapomorphic nature of the *Forcipiger*, *Hemitaurichthys*, and *Heniochus* intestinal coiling patterns seems to be questionable. The varia-

bilities of the patterns in these genera as well as in *Coradion* seem to reduce the phylogenetic significance of the intestinal coiling pattern regarding these genera. However, we learn that significant divergence from the basic chaetodontid pattern has repeatedly taken place as the chaetodontids evolve. Further studies on the intestinal coiling patterns of the above genera will allow us to recognize the species-specific and generic patterns. With this new knowledge we may be able to understand how these Type-5 patterns are related.

Closing remarks on the chaetodontid phylogeny

According to the above data, we believe that all chaetodontids have a common ancestor by sharing a synapomorphic kidney character with posterior kidney extensions on both sides of the first haemal spine. Except for *Forcipiger*, *Hemitaurichthys*, *Heniochus*, and *Johnrandallia*, the rest of the chaetodontids form a monophyletic group by sharing a Type-2 kidney. Within this group, *Chelmon* and *Chelmonops* are closely related by sharing a Type-4 intestinal coiling pattern. *Chaetodon* and *Parachaetodon* are monophyletic due to the lateral line character. Within this group, possessors of a Type-2 and -3 pattern (including the *Parachaetodon*, *Prognathodes* series of the *Chaetodon*, and some *Chaetodon* species) are closely related, leaving the systematic position of these *Chaetodon* spp. with a Type-1 intestinal coiling pattern unresolved. All *Chaetodon* species with a Type-3 pattern (not including the *Prognathodes* series) are monophyletic within the *Chaetodon-Parachaetodon* group. Accordingly, *Chaetodon* is not a monophyletic group. The exact phylogenetic positions of *Hemitaurichthys*, *Forcipiger*, *Heniochus*, *Johnrandallia*, *Amphichaetodon*, and *Coradion* cannot be resolved.

General discussion

Mok (1977) found that the acanthurid intestinal coiling patterns and intestinal length do not correlate with food habits. Chaetodontid food habits were studied by Hiatt and Strasburg (1960), Hobson (1974), and Reese (1977), to name a few. Chaetodontids are in many cases omnivores with vegetable matter composing part of their diet. They belong to one of three feeding categories (e.g., Reese, 1977): carnivores (and/or

obligative coral feeder), omnivores, and plankton feeders. In chaetodontids, different feeders can have the same intestinal coiling pattern. For instance, the carnivores (e.g., *Chaetodon punctatofasciatus*, *C. ornatissimus*, *C. trifascialis*, and *C. trifasciatus*; Hobson, 1974; Reese, 1977), the omnivores (e.g., *C. citrinellus*; Reese, 1977), and the plankton feeders (e.g., *C. kleinii*; Burgess, 1978) share a Type-2 pattern. Within a particular feeding category, many intestinal coiling patterns can coexist. Taking omnivores for instance, there are Type-1 pattern (e.g., *C. unimaculatus*), Type-2 pattern (e.g., *C. citrinellus*), and Type-3 pattern (e.g., *C. vagabundus*). We do not see a significant correlation between food habit and intestinal coiling pattern. However, it is interesting to note that many of the *Chaetodon* spp. with a Type-3 pattern are omnivores. Because of the above conclusion and that the intestinal length is considered to be associated with food habit, we do not expect a high correlation between intestinal length and intestinal coiling pattern. Our data show that this expectation is correct. It is not true that a long intestine will lead to a Type-3 pattern which includes the forward (or leftward) and downward foldings of loop **a** and is therefore considered as a complex pattern. Fishes with relatively similar intestinal lengths (64-mm in *C. argentatus* and 58-mm in *C. vagabundus*) may have Type-2 and -3 patterns, respectively. Fishes of similar body length but of different intestinal length can develop a similar pattern (e.g., the 87-mm *Chaetodon aya* with short intestine and the 60-mm *Parachaetodon ocellatus* with long intestine share a Type-2 pattern). In addition, fishes with a short intestine can develop different patterns. For instance, *Chaetodon modestus* has a Type-1 pattern, whereas *C. aya* has a Type-2 pattern instead. Based on these observations and correlations, we confer that intestinal coiling pattern has phylogenetic significance. It is also interesting to note that those chaetodontids in which loop **a** is not easily recognizable and does not coil in an orderly dextral pathway show higher individual and ontogenetic variations in their intestinal patterns. *Forcipiger*, *Hemitaurichthys*, *Heniochus*, and *Johnrandallia* provide examples of this character. In spite of these variations, species-specific characteristics of the pattern in these genera can still be identified in some cases.

The chaetodontid affinity of the genus *Microcanthus* was first questioned by Fraser-Brunner (1945) who believed that *Microcanthus* is related to *Atypichthys* and *Neatypus* of the family *Scorpididae*. This theory has been broadly adopted by recent ichthyologists. *Microcanthus strigatus*, *Atypichthys strigatus*, and *Neatypus obliquus* share the generalized perciform kidney type and intestinal coiling pattern (Type D1). The plesiomorphic character states of these structures are no evidence for their close affinities either to the Chaetodontidae or Scorpididae (or Kyphosidae).

The long-snouted *Forcipiger* and *Chelmon* pose a controversial systematic problem. Although these genera are occasionally considered closely related, most ichthyologists (e.g., Hubbs and Rehnitz, 1958; Hubbs, 1963; Nalbant, 1971, 1974; Burgess, 1978; Shen and Lam, 1979) agree that they are not derived from a common ancestor. Randall (1961) takes the view that *Forcipiger*, *Chelmon*, and *Chelmonops* are closely related groups. Interestingly, the intestinal coiling patterns and kidney morphology of these genera vary: *Forcipiger* resembles *Hemitaurichthys* in having a peculiar intestinal coiling pattern and in also possessing generalized chaetodontid kidney type. *Chelmon* and *Chelmonops* share the derived chaetodontid kidney type and intestinal coiling pattern. We, therefore, support the monophyly of *Chelmon* and *Chelmonops*. The proposal of Shen and Lam (1979) on the monophyly of *Chaetodon* and *Chelmon* was based on three interpretations: 1) the monophyly of *Chaetodon* (no evidence was given by these authors), 2) possession of a leftward folding in the anterior section of the intestine (e.g., a Type-3 pattern) is a plesiomorphic pattern for *Chaetodon* spp., 3) the leftward foldings in *Chelmon* and the ancestral *Chaetodon* pattern are homologous. Data from the present study falsify these interpretations. We also believe that *Forcipiger* may belong to a group in which *Hemitaurichthys* is also included. It becomes clear that the resemblance in snout morphology between *Forcipiger* and *Chelmon* is a case of convergence. Regarding the phylogenies of *Chelmon* and *Chelmonops* interpreted on the basis of the downward or backward folding at rear end of loop a, we take the following view. If this character occurs in the early ontogenetic stages

in *Chelmon* and *Chelmonops*, they will be more closely related to those *Chaetodon* spp. with Type-2 and/or Type-3 intestinal coiling patterns than to those with a Type-1 pattern. As such, the *Chaetodon-Parachaetodon* group becomes paraphyletic. This latter theory conflicts with the one supported by the lateral line character. We, therefore, predict that the downward or backward folding at the rear end of loop a which is absent in adult stages is absent at all ontogenetic stages of these genera.

Nalbant (1973) studied the morphology of the lateral line, subopercular suture, snout, scale pattern in the dorsal fin, and came to the conclusion that there are six main phyletic series within Chaetodontidae, namely, the series of *Forcipiger*, *Heniochus-Hemitaurichthys*, *Chelmon-Chelmonops*, *Coradion-Parachaetodon*, *Chaetodon nigrirostris* (now classified as *Johnrandallia nigrirostris*), and *Prognathodes-Chaetodon*. He further suggested that *Johnrandallia*, *Prognathodes*, and *Chaetodon* have a common ancestor. We found that many of the character states of the characters he studied overlap in most of these series. We are unable to find any synapomorphic character states unique to the members of each series.

The exact phylogenetic position of *Parachaetodon* cannot be further resolved by kidney and intestinal coiling morphology. It is interesting to notice that the swimbladder of *Parachaetodon ocellatus* is separated into a small anterior chamber and a larger posterior chamber by a bottle-neck region (personal observation). Shen and Lam (1979) noted a similar character state of the swimbladder division in *Chaetodon trifascialis*. The intestinal coiling patterns of *P. ocellatus* and *C. trifascialis* belong to a Type-2 pattern and this similarity will not create conflicting evidence regarding their possible affinity. Swimbladder morphology deserves further attention which might lead to new evidence concerning the systematic position of *Parachaetodon ocellatus*. The sister group of *Parachaetodon ocellatus* can either be a *Chaetodon* species (or *Chaetodon* spp.) with a Type-2 intestinal coiling pattern or the monophyletic group including all *Chaetodon* spp. with a Type-3 pattern.

Hubbs and Rehnitz (1958) came to the conclusion that *Chaetodon aculeatus* is more closely related to *C. aya* and its related species

(e.g., *C. falcifer* and *C. marcellae*) than to other chaetodontids. Nalbant (1965) erected a new genus *Bauchotia* for *C. aya*, *C. guyanensis*, *C. falcifer*, and *C. marcellae*. In his 1974 paper he treated this group as a subgenus of *Prognathodes*. With regard to the species interrelationships within *Prognathodes*, he stated, "Analysis of the skeleton of the dorsal fin in the species belonging to *Prognathodes* disclosed two evolutionary lines. The first consists of the species *C. marcellae* and *C. falcifer* in which the free pterygiophores are wide-set and remote from the lamina of pterygiophores 3 and 4; a second line would be represented by species of *C. aculeatus* and *C. aya* in which the first pterygiophores are almost fused and located next to the lamina 3 and 4." (Nalbant, 1974: 306). *C. aculeatus* and *C. aya* have a Type-2 intestinal coiling pattern. The patterns of *C. falcifer* and *C. guyanensis*, and *C. marcellae* await to be studied but we expect them also have the same pattern as the *C. aculeatus* and *C. aya*. It is clear from our data that the *Prognathodes* series is not so closely related to those *Chaetodon* spp. with a Type-3 intestinal coiling pattern as to either hypothetical ancestor of the latter group or those *Chaetodon* species or *Parachaetodon ocellatus* with a Type-2 pattern.

Burgess (1978) pointed out that the closest relatives of *Coradion* are *Chelmon*, *Chelmonops*, and *Chaetodon modestus* and its related species. This proposal was based on the occurrences of vertical banding in the body and a black membrane on the second dorsal spine in these genera. About the genus *Amphichaetodon*, he concluded that it has affinities to *Chelmonops*. Our data can neither reject the possible affinity of *Coradion-Chelmon-Chelmonops* nor *Amphichaetodon-Chelmon-Chelmonops*. However, they falsify the monophyletic relationship of *Chaetodon modestus* to either *Chelmon*, *Chelmonops* or *Coradion*.

Acknowledgments

We would like to thank Gareth J. Nelson, C. L. Smith, American Museum of Natural History; John R. Paxton, Helen K. Larson, Australian Museum, Sydney; J. E. Böhlke, Academy of Natural Sciences of Philadelphia; John E. Randall, Bernice P. Bishop Museum; William N. Eschmeyer, California Academy of Sciences; Walter Courtenay, Florida Atlantic University;

R. Grant Gilmore, Harbor Branch Foundation, Inc.; R. Rosenblatt, Scripps Institution of Oceanography; John Glove, South Australian Museum; Warren Burgess, TFH Publication, Co.; V. Springer, United States National Museum; David Caldwell, University of Florida; Jerry Allen and Barry Hutchins, Western Australian Museum for information, loans of specimens and their permission to dissect the specimens. The valuable suggestions of Michael Oliver, Yale University, and the time he spent in helping the senior author in search for references and specimens are most appreciated. Part of this study was conducted by the senior author (Mok) at the Ichthyology Department, American Museum of Natural History under the guidance of Gareth J. Nelson. The results were included in the Ph. D. dissertation of the senior author. The rest of the study was finished while the senior author was a postdoctoral fellow at the Harbor Branch Institution, Inc. We sincerely thank Gareth J. Nelson and R. Grant Gilmore for reading the manuscript and offering comments. This paper is Contribution No. 221 of the Harbor Branch Foundation, Inc.

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腎臓および腸の分化から見たチョウチョウオ科の系統

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チョウチョウオ科 (キンチャクダイ科, カゴカキダイ属, *Vinculum* 属は含まない) の系統を明らかにするために, 腎臓の形態および腸型の変異を調査・分類した. その結果 (1) 本科魚類は共通の祖先を持ち, さらに (2) フェヤッコ属, カスミチョウチョウオ属, ハタタテダイ属, *Johrandallia* 属を除いた残りのものは単系群を形成し, (3) ハシナガチョウチョウオ属と *Chelmonops* 属はごく近縁で, (4) チョウチョウオ属とテンツキチョウチョウオ属からなる単系群のうち, テンツキチョウチョウオとチョウチョウオ属の *Prognathodes* 亜属およびその他のいくつかの種とが特に近縁であり, (5) フェヤッコ属, カスミチョウチョウオ属, ハタタテダイ属, *Johrandallia* 属は腎臓の形態は似ているが, 単系群であるかどうかはなおはっきりしないなどのことが示唆された. 以上の結果に基づきチョウチョウオ科の系統を推論し, 従来の仮説と比較した.