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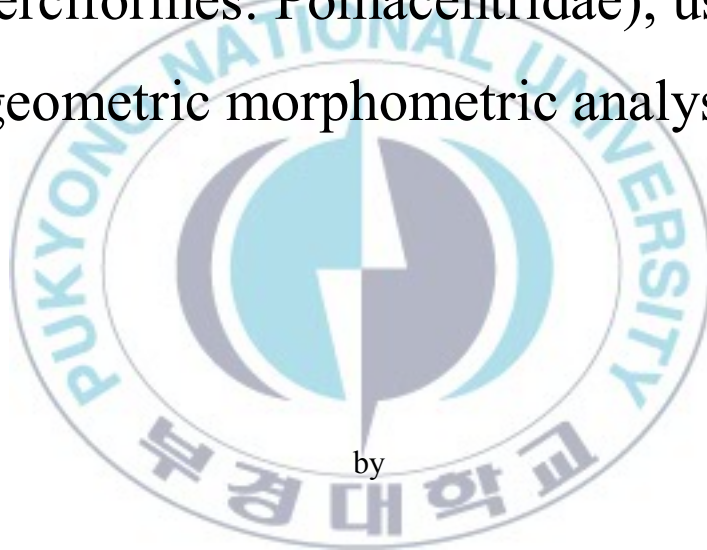
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Thesis for the Degree of Master of Science

Comparison of jaw structure between
Chromis notata, *C. fumea* and *C. albicauda*
(Perciformes: Pomacentridae), using
geometric morphometric analysis



by

Young Sun Song

Department of Marine Biology

The Graduate School

Pukyong National University

February 2014

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연무자리돔 및 흰꼬리노랑자리돔
(농어목:자리돔과)의 턱구조의 비교]

Advisor: Prof. Jin Koo Kim

by

Young Sun Song

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Young Sun Song

Approved by:

(Chairman) Dr. Won Gyu Park

(Member) Dr. Byung Jik Kim

(Member) Dr. Jin Koo Kim

February 21, 2014

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기하학적 형태분석 방법을 이용한 자리돔, 연무자리돔 및 흰꼬리노랑자리돔의 턱구조의 비교

송 영 선

부경대학교 대학원 해양생물학과

요 약

본 연구는 자리돔, 연무자리돔 및 외집단으로 흰꼬리노랑자리돔 총 세 종의 섭이골격구조(전상악골, 주상악골, 치골, 관절골 및 각골, 하인두골)를 기하학적 형태분석방법을 이용하여 비교, 분석하였다. 연구 결과를 토대로 이들의 섭이방법과 분포차이 나아가 세 종간의 진화역사를 함께 추론하였다. 골격분석결과, 세 종은 전상악골과 치골, 관절골 및 각골의 형태에서 명확한 차이를 나타냈다. 악골차이의 결과는 이들의 섭이방식 과도 연관되었다. 자리돔은 연무자리돔이나 흰꼬리노랑자리돔보다 두꺼운 아래턱을 가지고 있어 안정적인 힘을 제공받을 수 있기 때문에 단단한 먹이를 섭이하는데 용이할 것으로 보여진다. 연무자리돔은 자리돔이나 흰꼬리노랑자리돔과는 달리 긴 전상악골 상행돌기를 가져 윗턱의 전방 신출에 용이하며 얇은 아래턱은 먹이를 씹어삼키기 보다는 활동성 있는 먹이를 효율적으로 포획하는데 적응한 기능형태로 보여진다. 흰꼬리노랑자리돔의 윗턱은 자리돔과 유사한 반면, 아래턱은 연무자리돔의 형태와 비슷하였으나 대부분의 골격은 두 종보다 크고 발달되었다. 세 종은 양턱과 상하인두골은 끝이 날카롭고 얇은 원뿔니를 가지며, 새파는 수가 많고 새파 사이 간격이 좁은 형태 특징으로 보아 동물플랑크톤 섭이에 유용하도록 적응한 형태라고 할 수 있다. 악골 형태의 진화방향은 이들의 종분화와 밀접한 연관성을 가지며 일부 그 역사를 보여준다. 오래 전 공동기원으로부터 분화가 이루어질 때, 연무자리돔은 일찍이 열대-아열대성의 적도 쪽으로 이동하면서 종 분화가 빠르게 진행된 것으로 사료되며, 반대로 자리돔은 원시 조상형이 형질을 오랜기간 보유하고 있었으나, 최근에 분화되면서 대만에서 한국, 일본으로 북상하게 됨에 따라 연무자리돔보다는 온대와 한대에 더 적응되어 진화한 종으로 보여진다.

I. Introduction

1. Background

The Pomacentridae widely distributes throughout temperate, tropical, and subtropical seas and consist of 387 species in 28 genera worldwide (Froese and Pauly, 2013). In species number, this family represents the third most abundant group in the coral reef community after the Gobiidae (>1,500 species) and the Labridae (>450 species) (Wainwright and Bellwood, 2002). The various body shapes and color patterns vary with their habitat environment.

In fishes, the jaw shapes have been mainly studied in cichlid and labrid species (Albertson et al., 2003; Waltzek and Wainwright, 2003; Stewart and Albertson, 2010), and the other taxa such as Pomacentridae and Serranidae being actively studied (Weaver, 2001; Grubich et al, 2008). Jaw shape related to diet, clearly appears to be a major driving force of morphological evolution in damselfishes (Emery, 1973; Gluckmann and Vandewalle, 1998; Aguilar-Medrano et al., 2011). Especially, jaw morphology in damselfishes is tightly linked to trophic ecology (Frederich et al., 2008; Frederich and Vandewalle, 2011), and thus a morpho-functional analysis of trophic characters offers an excellent system for testing whether pomacentrids have experienced iterative adaptive radiations (Frederich et al., 2009; Frederich and Vandewalle, 2011).

Damselfishes are commonly recognized three major trophic groups and prey capture methods: pelagic feeders (ram and/or suction feeding), and benthic feeders

(grazing algae or biting coral polyps), and intermediate groups (planktonic prey, small benthic invertebrates, and algae in variable proportions) (Allen, 1991; Cooper and Westneat, 2009; Frederich et al., 2013). Among them, the genus *Chromis* species are known as pelagic feeders mainly feeding on zooplankton using suction feeding (Preys are sucked into predators mouths) and/or ram feeding (Lunge feeding; predators overtake the preys by moving with an open mouth) (Lauder, 1980; Liem, 1980; Allen and Erdmann, 2012; Frederich et al., 2013). If oral morphology appears to determine the fundamental trophic niche (Wainwright and Richard, 1995), dietary shifts could be associated with morphological modifications of the feeding apparatus (Wainwright, 1991; Liem, 1993). Also, difference between feeding methods can be linked to the shape of jaw skeletal units. In addition, the phylogenetic relationship indicates the part of the similarity in the interspecific morphology and ecology (Motta, 1988; Douglas and Matthews, 1992). In fish, geometric morphometric analysis (GMA) can apply to various research fields such as the comparison of interspecific morphology and populations, and morphological variation during the evolution (Adams, 1999; Cavalcanti et al., 1999; Cadrina and Friedland, 1999; Albertson and Kocher, 2001; Helland et al., 2009; Toscano et al., 2010; Requieron et al., 2012). Frederich et al. (2008, 2012) performed the various studies using GMA in pomacentridae,.

Among the genus *Chromis* species in Korean waters, *C. notata* and *C. fumea* are very similar to the external shape (i.e. Two spiniform procurrent caudal rays, etc.) and the part of the skeletal shape (i.e., sphenotic, palatine, posttemporal, etc.), whereas quite distinguished from *C. albicauda* (Kim and Kim, 1996; 1997; Song et al., 2013). *C. notata* has a relatively limited distribution, including Taiwan,

China, Ryukyu Islands, Southern Japan, whereas *C. fumea* is widely distributed in Indo-West Pacific, eastern edge of the Indian Ocean, Australia, etc. (Allen, 1991; Froese and Pauly, 2013). Distribution difference estimates that it is affected by eco-morphological perspective, such as feeding activity or diet as well as environmental factors such as water temperate or salinity.



2. Purpose of this study

The purpose of the present study is to compare and analyze the jaw skeletal structure (premaxilla, maxilla, dentary, angular, retroarticular, and upper and lower pharyngeal jaw) of three species in detail using GPA, and to reveal the relationship between jaw skeletal structures and feeding methods and more intend to re-reveal evolutionary history between them.



II. Materials and methods

1. Sampling and data collection

Three species in the genus *Chromis*: *C. notata* (Temminck and Schlegel, 1843) ($N = 91$; total length, TL: 76~131 mm); *C. fumea* (Tanaka, 1917) ($N = 87$; total length, TL: 83~121 mm); *C. albicauda* Allen and Edrmann, 2009 ($N = 21$; total length, TL: 97~144 mm); were collected with lift nets from Bomok-port, Seogwipo-si, Jeju-do in March and April 2013. All specimens promptly were transferred to the laboratory after sampling. The total length (TL) of fishes was measured to the nearest 0.1 millimeter, and then specimens were stored at -20°C in the freezer. All specimens were adult or sub-adult, being a size sufficiently close to their maximum total length (TL) in order to avoid any problems relating to possible differences in jaw skeletal shape in relation to their ontogeny (Table 1) (Clements and Choat, 1993; McCormick, 1998; Monteiro et al., 2005).

Table 1. *Chromis* Species examined in this study

Species	<i>C. notata</i>	<i>C. fumea</i>	<i>C. albicauda</i>
N	91	87	21
SAn	30	30	21
TL ^{max}	170	130	175
TL ^{mm}	76 ≤ TL ≤ 131	83 ≤ TL ≤ 121	97 ≤ TL ≤ 144

N, number of specimens; SAn, number of skeletal analysis; TL^{max}, maximum total length reported in Allen and Edrmann, 2012 (in mm); TL^{mm}, range of total length of specimens (in mm).



A)



B)



C)



Fig. 1 Photos of specimens, (A) *C. notata*, PKU 9038; (B) *C. fumea*, PKU 5528; (C) *C. albicauda*, PKU 5803.

2. Skeletal bone dissection

In order to compare jaw skeletal shape among species, in 30 individuals *C. notata* and *C. fumea* used to dissect and *C. albicauda* used 21 individuals. Specimens were removed their tissue after boiling for about 5 min, and then were dissected five skeletal units (premaxilla, maxilla, dentary, angular and retroarticular, upper and lower pharyngeal jaw) in sequence. The dissected skeletal units were soaked in 1 % KOH solution to remove the residual tissue and to clear bones. At this point, it avoided being removed the teeth on the premaxilla, the dentary, upper and lower pharyngeal jaw by controlling the amount of KOH and clearing time. After clearing, it was stained with alizarin red-S for 1 hour in order to display the osseous skeleton (Taylor and Van Dyke, 1985), and then preserved in glycerol or 70% alcohol.

3. Skeletal bone description

Skeletal shape observed and sketched in detail using the stereomicroscope (Olympus SZX-16. Japan) with camera lucida attachment. Counts and measurements were conducted according to the methods of Fredefich et al. (2008). The jaw skeletal units were also observed and photographed using the photography system for the microscope and the attached digital camera (Motic Moticam Pro 205A, China).

4. Geometric morphometric analysis and Statistics

i. Landmarks set

Size and shape vary of (1) the Premaxilla, (2) the Maxilla, (3) the Dentary, (4) the Angular and retroarticular, (5) the Upper pharyngeal jaw, (6) the Lower pharyngeal jaw were studied using landmark-based geometric morphometric methods in order to quantify the jaw skeletal units shapes (Bookstein, 1991; Rohlf and Marcus, 1993; Marcus et al., 1996). Each skeletal unit was analyzed and photographed in lateral view with camera (Motic Moticam Pro 205A, China). In each species, the *x*- and *y*-coordinates of 7 homologous landmarks were defined on the premaxilla, 10 on the maxilla, 9 on the dentary, 10 on the angular and retroarticular, 4 on the upper pharyngeal jaw and 8 on the lower pharyngeal jaw (Fig. 2). These were chosen according to their accuracy of digitization and homologization, as well as in order to represent the unit and its parts as accurately as possible. Also, the name of skeleton units was designated according to Kim and Kim (1997) and Frederich et al. (2008): An = angular, Arp = angular process of premaxilla, Asp = ascending process of premaxilla, D = dentary, Denp = dentigerous process, Lp = lateral process, LpgJ = lower pharyngeal Jaw, M = maxilla, Pasp = postmaxilla process of premaxilla, Pm = premaxilla, Retroar = retroarticular, UpgJ = upper pharyngeal Jaw (Fig. 2). Landmarks were localized on all of the specimens using an image analysis program, and the coordinates of landmarks were digitized using Morphologika2 and Morpho J program.

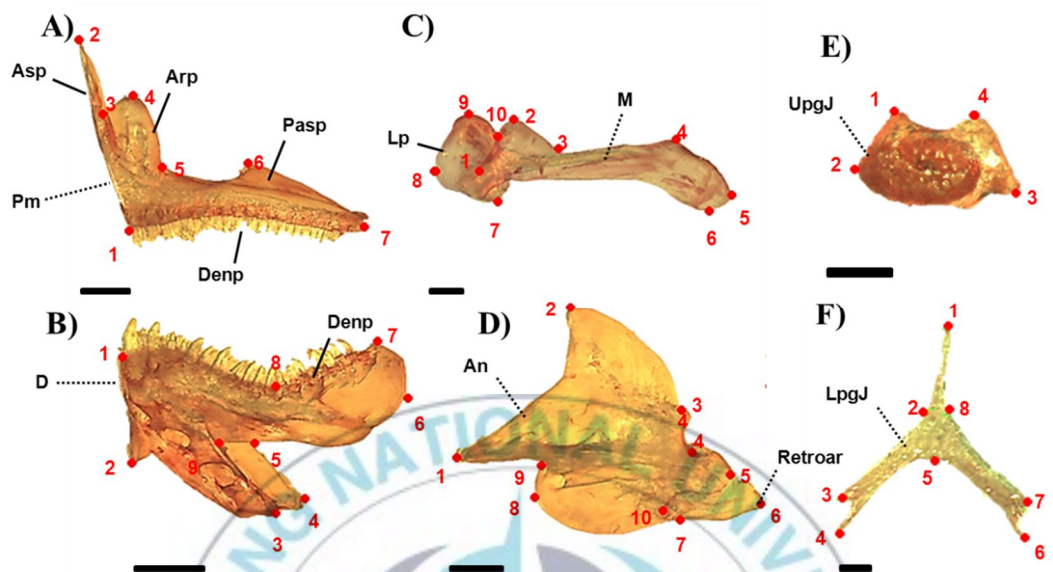


Fig. 2 Localization of the different landmarks (LM) on; The number of landmarks A) Premaxilla, 7 ; B) Dentary, 9; C) Maxilla, 10 ; D) Angular and Retroarticular, 10; E) Upper pharyngeal jaw, 4; F) Lower pharyngeal Jaw, 8.

ii. GPA (Generalized procrustes analysis)

Landmark configurations of each of the four structures were superimposed using generalized procrustes analysis (Rohlf and Slice, 1990) to remove the non-shape variation (scale, orientation, translation) and to obtain the consensus configuration (average) of the landmarks for each skeletal unit. This procrustes procedure allows the size and shape to be considered as two independent components. GPA was computed using Morphologika 2 program (O'Higgins and Jones, 2006).

iii. PCA (Principal component analysis)

A principal components analyses were used, as exploratory methods, to find hypothetical variables (components) that account for as much of the variance in the morphological data which consists of the coordinates of landmarks (Davis, 1986), and used as descriptors of shape variation using Morphologika 2 program (O'Higgins and Jones, 2006). This method is performed to estimate the diagnostic characters having a high degree of contribution when distinguishing between groups. The results forming on the axes of two-dimensional (PC1 and PC2) indicate the relative shape difference between groups.

iv. CVA (Canonical variate analysis)

Canonical variate analysis was performed to evaluate the shape variation

between groups using Morpho J program (Klingenberg, 2011). The results indicate on the axes of two-dimensional (CV1 and CV2). The configuration of deformation grids and wire frame graph were visualized on coordinate of two-dimension.



III. Results

1. Jaw bones composition

All of three species have the upper jaw comprising premaxilla and maxilla, and the lower jaw comprising dentary and angular and retroarticular, and the upper and lower pharyngeal jaws around the throat behind the oral cavity. Especially, the average size of *C. albicauda* was larger than *C. notata* and *C. fumea*.

i. Premaxilla

Premaxilla was similar to “L” shape like as the boomerang on the whole. Partial name of premaxilla as follows: Dentigeorus process (Denp) with teeth; Ascending process of premaxilla (Asp) is a long element linked with the anterior dentigeorus process; Angular process of premaxilla (Arp) is crest part sited on just behind the Asp; Postmaxilla process of premaxilla (Pasp) is a posterior crest part. The groove between dentigeorus process and ascending process was related to moving the upper jaw by linking the lateral process of maxilla.

In the results of the comparison of groove between *C. notata* and *C. fumea*, the latter was significantly deeper than former. The dentition was divided into outer and inner rows. The outer row was arranged in a row with conical teeth in regular. The number of teeth was 22 to 27 in *C. notata*, 21 to 28 in *C. fumea*, and 21 to 27 in *C. albicauda*. Whereas, the inner row was irregularly arranged in rows with

small conical teeth (Fig. 3). According to the average ratio values for head length (HL) in each bone element size, the results were significant differences in the length of ascending process, the distance between the tip of ascending process and the angular process, the height of angular process, and the angle size ($^{\circ}$) between ascending process and dentigeorus process (Table 2). *C. fumea* had long ascending process, long distance between the tip of ascending process and angular process, deep groove between dentigeorus process and ascending process, and high angular process than *C. notata*. Whereas, *C. notata* had the big angle ($^{\circ}$) between ascending process and dentigeorus process in addition to the high degree of the slope of ascending process. *C. albicauda* had large size of skeletal units than the others, and shown the intermediate shape between *C. notata* and *C. fumea* but the angle ($^{\circ}$) between ascending process and angular process was similar to the shape of *C. notata*.

ii. Maxilla

The maxilla was claviform which its posterior tip was bent. Anterior part is the lateral process, which was slightly twisted and bent, and the helical form increases the linkage to the space between ascending process and angular process. Especially, it is highly related to moving the upper jaw. Posterior part was the twist cylindrical shape, and its tip was downward. Lateral process was three-dimensional but its posterior part was flat. *C. fumea* had a short and thin shape. *C. albicauda* appear in the broadest and largest joint region of the lateral process, and also its shape is the largest and thicker than the others (Fig. 4). According to the

average sizes for head length in each bone elements, the results are no significant differences among three species.

iii. Dentary

Dentary is the main bone consisting of the lower jaw. It included in the dentigeorus process with teeth. The dorsal shape of dentigeorus process was similar to “S” shape like as a wave. Its anterior part had three sensory pore with various sizes and shapes. Sometimes, first sensory pore opened towards the front. Its posterior part was like as “V” shape and linked to the angular and retroarticular unit by the Meckelian cartilage. The region of Meckelian cartilage was sited in the upper-behind of the first sense pore. The teeth of dentigeorus process were divided into the outer and inner rows, and inner was arranged in rows with conical teeth irregularly. The number of teeth on outer row was 17 to 23 in all of three species. The anterior teeth were larger and developed than those of the posterior part (Fig. 5). According to the averages sizes for head length in each bone elements, the length of the ventral region of the dentary was different, and also that indicated the height of the dentary. *C. notata* had the longest ventral region. And *C. notata* appeared the strongly developed dentary whereas *C. fumea* had relatively low dentary. *C. albicauda* was similar to the shape of *C. fumea* but had the border than *C. notata* and *C. fumea* in the width of dentary (Table 2).

iv. Angular and Retroarticular

Angular and retroarticular was fused into single unit each other. Retroarticular was located in below the posterior angular. Most of the retroarticular were covered by the angular. Anterior part of angular was linked in the posterior of the dentary, and its shape was the projecting process. The length of the projecting process was long and it increases the linkage force with the dentary. The face of the angular and retroarticular was concave like as shell shape. And retroarticular formed triangle, but the shape and size were irregular (Fig. 6). According to average sizes for head length in each bone elements, *C. notata* and *C. fumea* were similar to the height of the angular and the length of the projecting process. *C. albicauda* was larger than the others in all of the parts. However, *C. notata* and *C. fumea* were possible to distinguish by the size of retroarticular. The size of the retroarticular in *C. fumea* was larger than *C. notata* and similar to that of *C. albicauda*.

v. Upper and lower pharyngeal jaw

Pharyngeal jaw was located in the intermediate space of oral cavity toward to the throat. It was consisted of the upper and lower pharyngeal jaws and it had teeth. The upper pharyngeal jaw was trapezoid. The lower pharyngeal jaw was a triangle form which is concave on the central in each face, and it was divided into the upper region with teeth and lower region consisting of supporting bone. The tip of each corner in the lower region was elongated. The out-row teeth in the

upper region were very thin and long, and its tip was slightly sharp. In contrast, the blunt and short teeth were dense in the inner-rows. Upper pharyngeal jaw was consisted of the part of left and right, and that was shaped like as the kidney bean. The shape between three species was significant differences that *C. notata* appeared to equilateral triangle shape, whereas *C. fumea* and *C. albicauda* appeared to isosceles triangle shape (Fig. 7–8).



Table 2. Measurements of the jaw bones for three *Chromis* species.

Measurement (each regions % in HL)		<i>C. notata</i>	<i>C. fumea</i>	<i>C. albicauda</i>
Part of jaw bones	Each region	n=30	n=30	n=21
Premaxilla (% in HL, except for *)	1-7	24.8-29.8 (28.2)	25.5-30.1 (28.6)	18.6-42.8 (28.1)
	1-2	20.5-24.8 (22.7)	22.8-28.2 (25.3)	15.1-32.8 (23.6)
	2-3	6.8-10.4 (9.0)	9.7-14.8 (11.4)	6.0-13.3 (8.9)
	3-4	5.5-7.0 (6.3)	5.2-6.7 (5.9)	3.9-8.0 (5.7)
	2-7	36.4-42.7 (40.7)	37.7-44.3 (42.2)	26.7-59.1 (40.4)
	*Asp % in Denp	72.4-86.7 (80.6)	81.4-97.0 (88.6)	75.2-95.6 (84.3)
	The Arp height	12.9-16.7 (15.3)	16.8-21.6 (19.0)	11.2-23.5 (16.6)
	The Pasp height	5.8-7.3 (6.5)	5.4-7.8 (6.7)	3.9-8.0 (5.7)
*The angle (°) of Asp and Denp		98.1-114.1 (106.7)	87.2-109.7 (98.6)	101.6-119.6 (107.3)
Maxilla (% in HL)	5-8	33.5-39.3 (37.3)	30.3-45.5 (37.1)	32.9-56.3 (43.4)
	3-8	12.8-15.8 (14.8)	11.9-18.9 (14.5)	13.6-26.0 (19.3)
	3-5	21.1-25.6 (23.7)	19.4-28.9 (23.7)	19.8-33.3 (26.4)
	The height of Lp	9.7-13.9 (12.4)	10.2-16.1 (12.6)	12.6-23.8 (17.6)
Dentary (% in HL Except for *)	1-2	7.2-9.9 (8.5)	5.1-6.9 (6.2)	3.6-8.4 (5.7)
	1-7	20.4-23.5 (22.0)	18.8-23.5 (22.2)	14.4-34.0 (22.9)
	*1-2 % in Denp	33.9-43.5 (38.4)	21.6-32.4 (28.1)	22.9-26.2 (24.8)
Angular and Retro- articular (% in HL)	1-6	30.9-37.7 (35.4)	36.0-47.8 (41.9)	23.1-46.3 (34.4)
	1-9	8.3-12.3 (10.6)	10.7-13.4 (12.1)	8.2-14.0 (10.9)
	6-10	6.4-12.3 (10.7)	10.6-18.6 (15.0)	5.7-15.5 (10.7)
	The An height	20.0-23.4 (21.9)	20.6-32.4 (26.0)	12.8-32.0 (21.6)
Upper pharyngeal jaw (% in HL)	1-2	4.8-6.9 (5.8)	4.5-6.5 (5.7)	5.9-10.4 (7.7)
	1-4	5.1-6.3 (5.6)	4.3-6.7 (5.5)	5.4-10.9 (7.4)
	2-3	11.2-12.7 (11.9)	10.5-12.4 (11.5)	11.8-20.4 (15.3)
	3-4	5.5-7.2 (6.6)	6.1-7.2 (6.6)	6.4-10.3 (8.9)
Lower pharyngeal jaw (% in HL)	1-4	24.5-28.4 (26.3)	22.9-27.9 (25.9)	26.7-40.7 (34.2)
	4-6	19.7-23.7 (21.7)	19.4-25.0 (22.2)	24.5-34.7 (30.1)
	6-8	23.5-27.6 (25.3)	21.0-26.9 (24.6)	26.5-37.5 (32.3)

Parentheses indicate average

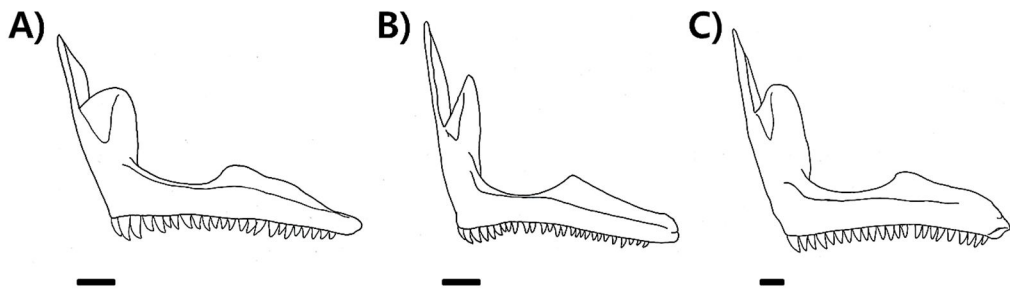


Fig. 3 Lateral view of premaxilla. (A) *Chromis notata* (B) *Chromis fumea* (C) *Chromis albicauda*. Scale indicates 1 mm.

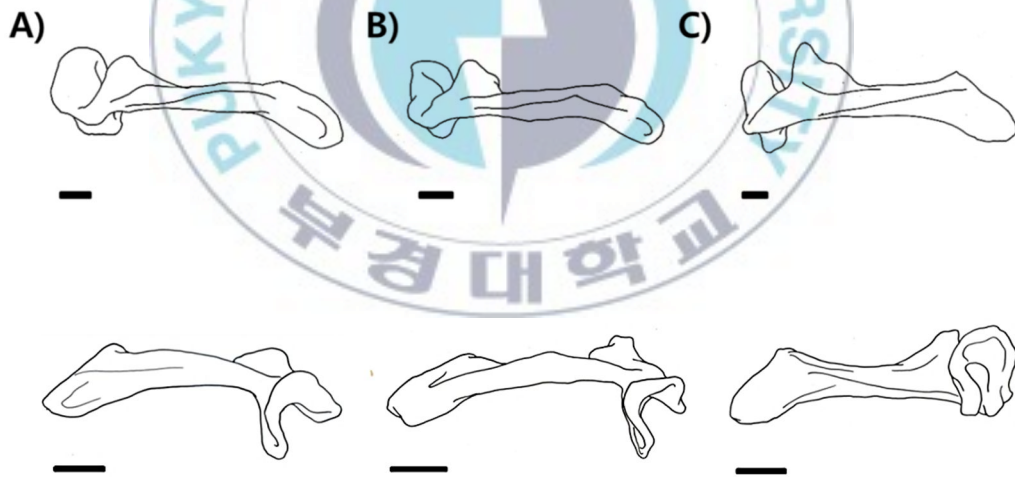


Fig. 4 Lateral (above) and medial (below) view of maxilla. (A) *Chromis notata* (B) *Chromis fumea* (C) *Chromis albicauda*. Scale indicates 1 mm.

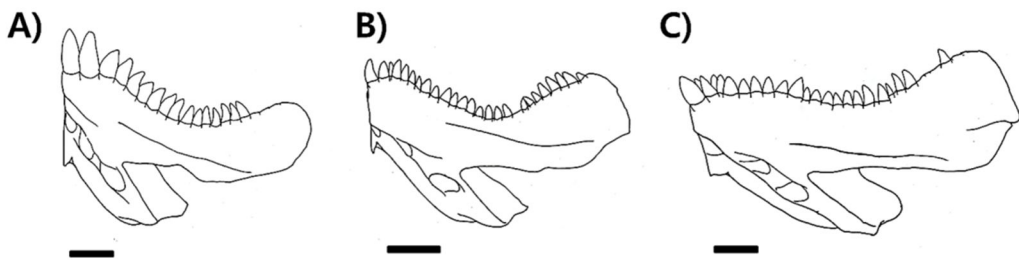


Fig. 5 Lateral view of dentary. (A) *Chromis notata* (B) *Chromis fumea* (C) *Chromis albicauda*. Scale indicates 1 mm.

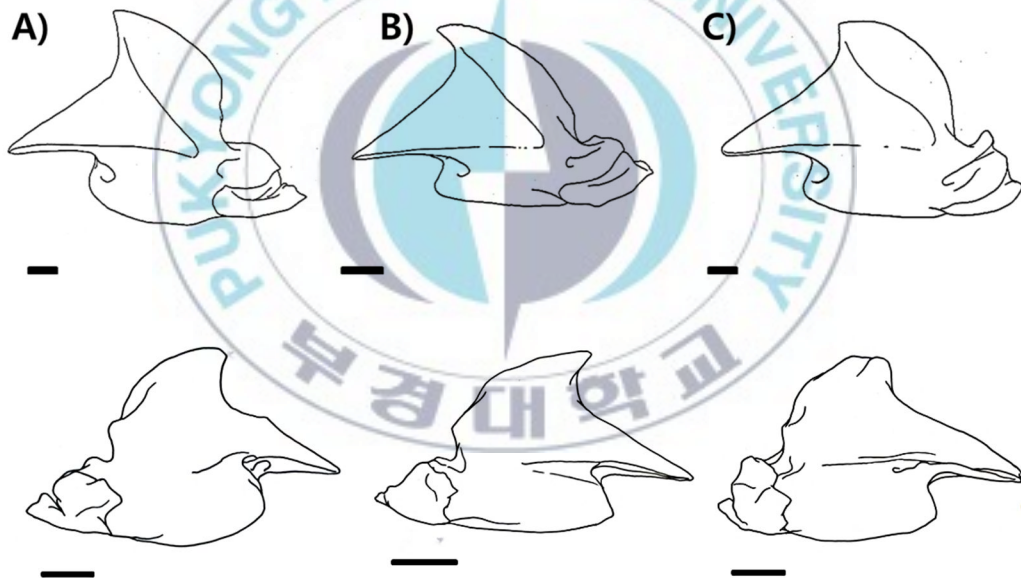


Fig. 6 Lateral (above) and medial (below) view of angular and retroarticular. (A) *Chromis notata* (B) *Chromis fumea* (C) *Chromis albicauda*. Scale indicates 1 mm.

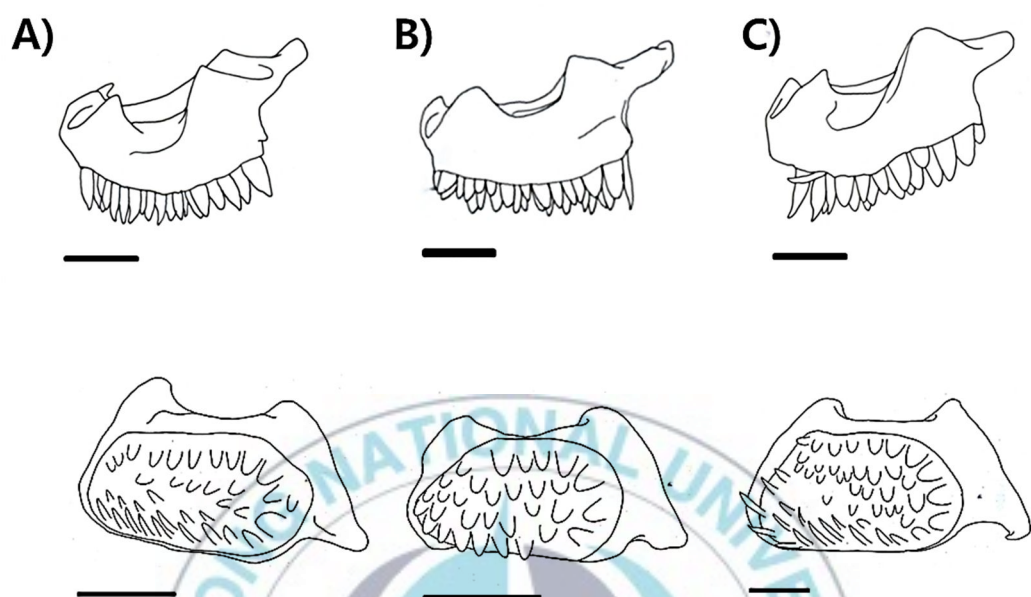


Fig. 7 Lateral (above) and dorsal view (bellow) of the upper pharyngeal jaw. (A) *Chromis notata* (B) *Chromis fumea* (C) *Chromis albicauda*. Scale indicates 1 mm.

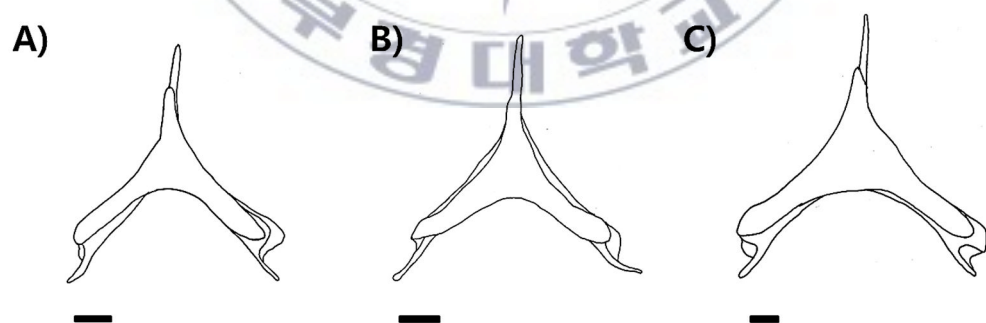


Fig. 8 Dorsal view of lower pharyngeal jaw. (A) *Chromis notata* (B) *Chromis fumea* (C) *Chromis albicauda*. Scale indicates 1 mm.

2. Geometric morphometrics of jaw bones

i. PCA

Main shape variations could be examined by distribution of specimens in the space defined by the axes PC1 and PC2 (Figs. 9–14). Intraspecific shape variation existed in all skeletal structures.

For the premaxilla, the first two PCs accounted for 73.2% of the shape variation (PC1=60.5%, PC2=12.7%) (Fig. 9). Two groups were distinguished along the PC1 axis. The first included only *C. fumea* and the second forms one group with *C. notata* and *C. albicauda*. Main shape differences between two groups were due to the groove between the ascending process and angular process of premaxilla. *C. notata* was proportionally longer than others (LM 2, 3, and 4). More specifically, these differences were mainly explained by the comparatively short ascending process of premaxilla (LM 1 and 2) and the large angle size (°) between ascending process and dentigerous process (LM 1, 2, and 7) in *C. notata*. *C. albicauda* was intermediate shape, and more similar to the premaxilla of *C. notata* (Fig. 9).

For the maxilla, the shape variation explained by PC1 and PC2 is 60.5% (PC1=40.5% and PC2=20.0%) of the total variation (Fig. 10). Two groups were distinguished along the PC axis, a first grouping *C. notata* and *C. fumea* in broad distribution, a second including only *C. albicauda*. The main shape difference between two groups was due to the expanded joint region of the lateral process of maxilla (LM 1, 2, 3, 8, 9, and 10). *C. notata* and *C. fumea* shared the similar shape, and *C. notata* had the narrower lateral process and *C. albicauda* had the broadest

and thickest lateral process (LM 3 and 8) (Fig. 10).

On the level of dentary (Fig. 11), the PC1 and the PC2 respectively accounted for about 36.4% and 26.2% of the total shape variation. In this shape space, *C. notata* and *C. fumea* were directly opposite to the each other on the PC2 axis rather than PC1 axis. The main shape difference between the two species was due to the length of symphysis mandible which is the ventral region of the dentary (LM 1 and 2). *C. notata* possessed the longest ventral region of dentary whereas *C. fumea* possessed the shortest ventral region of the dentary and the relatively short dentigeorus process (LM 1 and 7). *C. albicauda* and *C. fumea* shared the similar dentary shape (Fig. 11).

Concerning the angular and retroarticular, PC1 and PC2 define 63.7% (PC1=39.4% and PC2=24.3%) of the shape variation (Fig. 12) and allowed the discrimination of three groups. Along the PC1 axis, *C. notata* was isolated from *C. fumea*. PC2 axis permitted to the isolation of *C. albicauda*, *C. notata* and *C. fumea*. Main shape differences between *C. notata* and *C. fumea* were due to the size of retroarticular (LM 5, 6, 7, and 10) and the size of the posterior part in angular linking to the quadrate (LM 3 and 4). *C. albicauda* shown the lower shape than the others. The shape of *C. notata* was higher angle and retroarticular than *C. fumea* and *C. albicauda* (Fig. 12).

Concerning the upper pharyngeal jaw, the first two PCs accounted for 63.5% of the shape variation (PC1=33.4% and PC2=30.1%). All of three species were similar to the shape of that (LM 1, 2, 3 and 4) (Fig. 13).

For the lower pharyngeal jaw, the first two PCs accounted for 57.1% of the shape variation (PC1=31.3% and PC2=25.8%) (Fig. 14). According to the PC1 axis, *C.*

notata and *C. albicauda* were distinguished by the width of the dentigeorus process (LM 1, 2, 3, 6, 7, and 8). *C. fumea* was located in the intermediate space (Fig. 14).



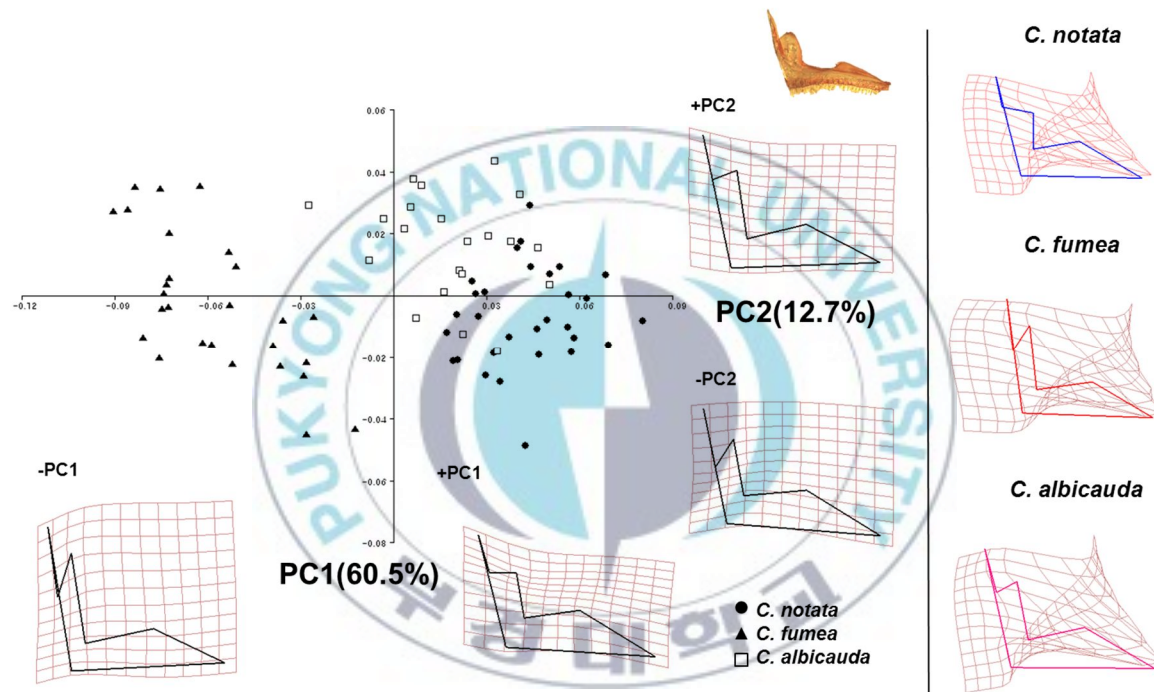


Fig. 9 Scatter plot of principal score 1 and 2 (PC1 and PC2) of the Premaxilla. Morphologika2 Deformation grids indicate shape variation represented by PC1 and PC2 (minimal (-PC) and maximal (+PC) values).

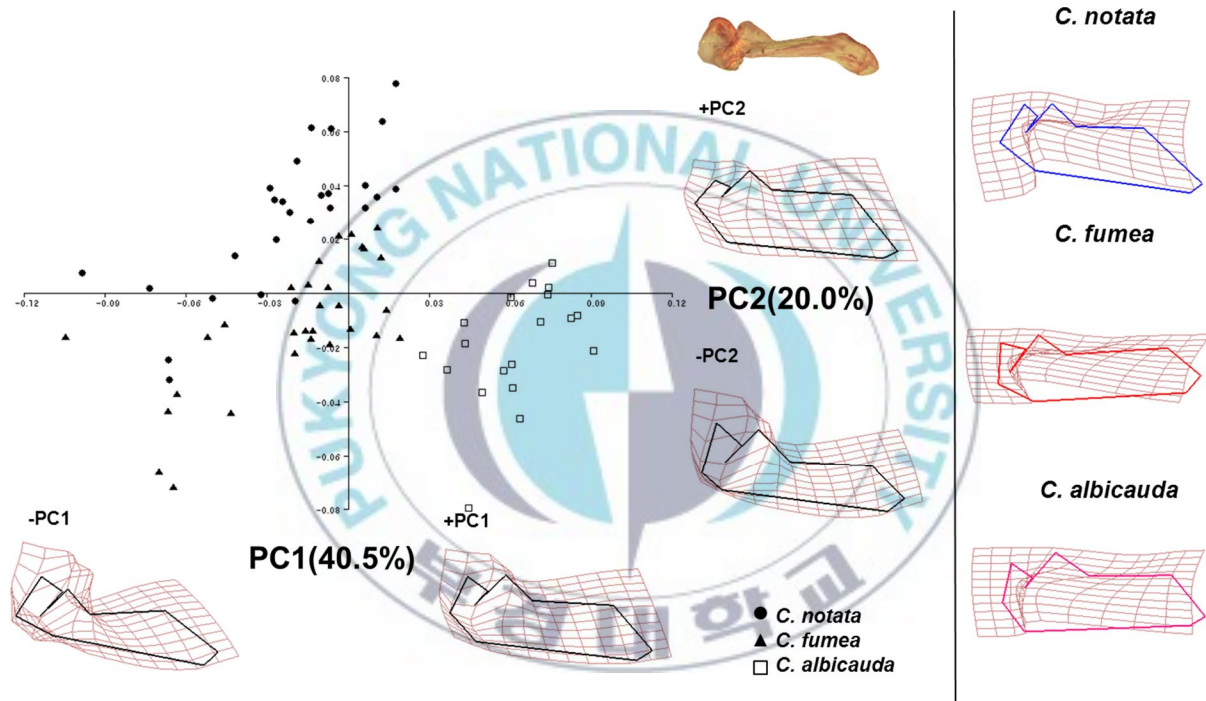


Fig. 10 Scatter plot of principal score 1 and 2 (PC1 and PC2) of the Maxilla. Morphologika2 Deformation grids indicate shape variation represented by PC1 and PC2 (minimal (-PC) and maximal (+PC) values).

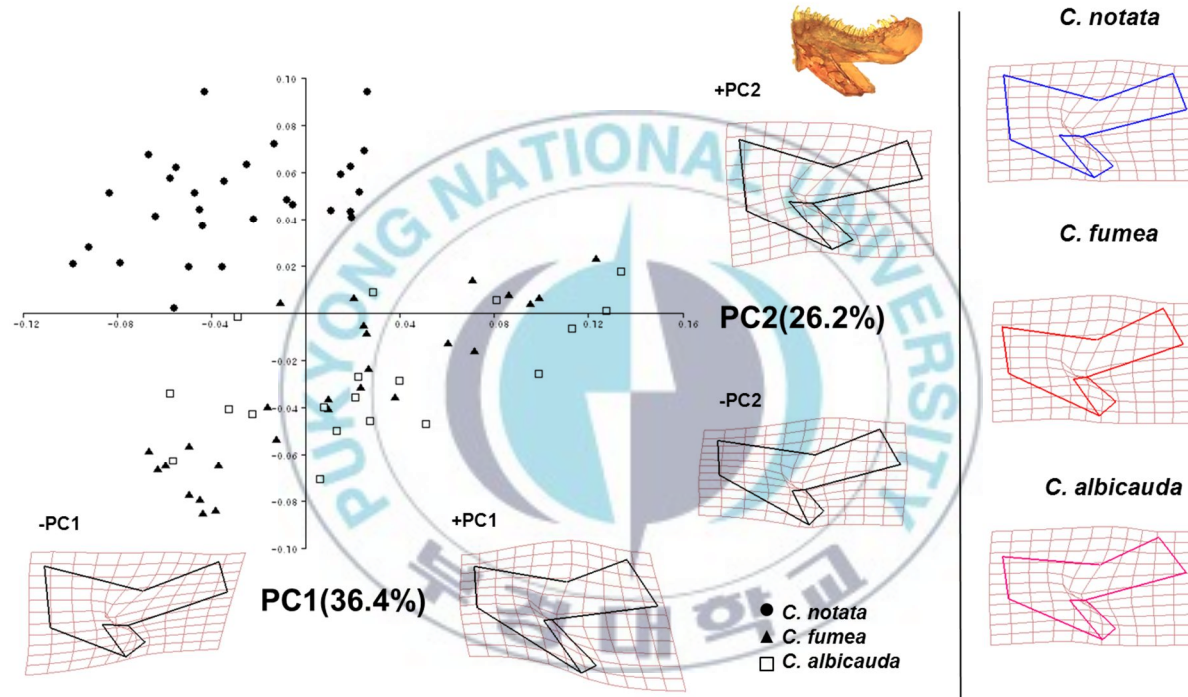


Fig. 11 Scatter plot of principal score 1 and 2 (PC1 and PC2) of the Dentary. Morphologika2 Deformation grids indicate shape variation represented by PC1 and PC2 (minimal (-PC) and maximal (+PC) values).

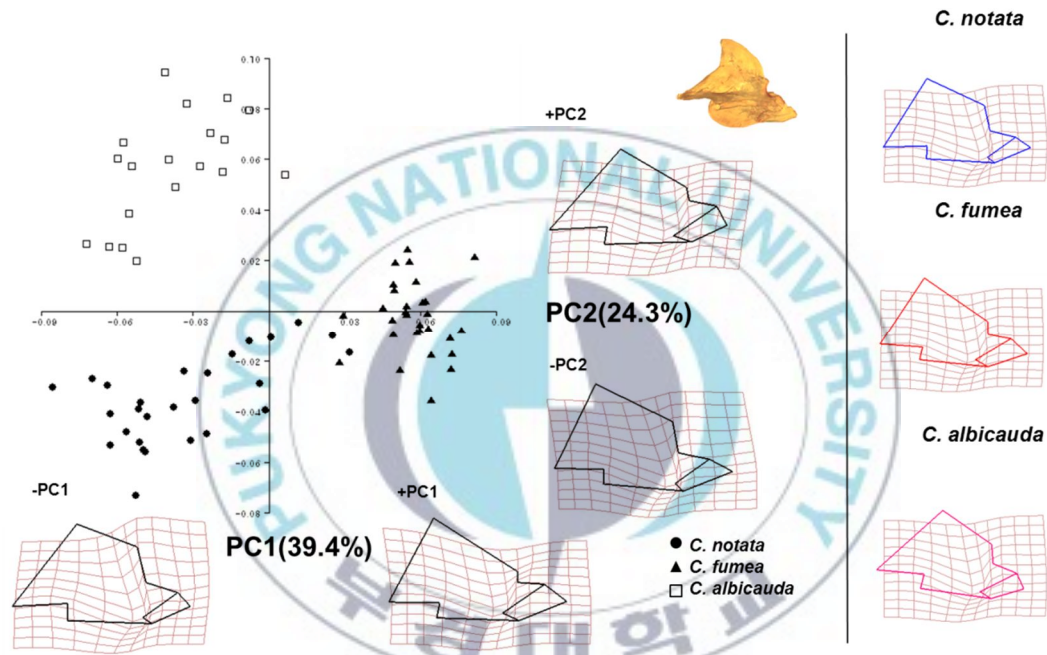


Fig. 12 Scatter plot of principal score 1 and 2 (PC1 and PC2) of the Angular and Retroarticular. Morphologika2 Deformation grids indicate shape variation represented by PC1 and PC2 (minimal (-PC) and maximal (+PC) values).

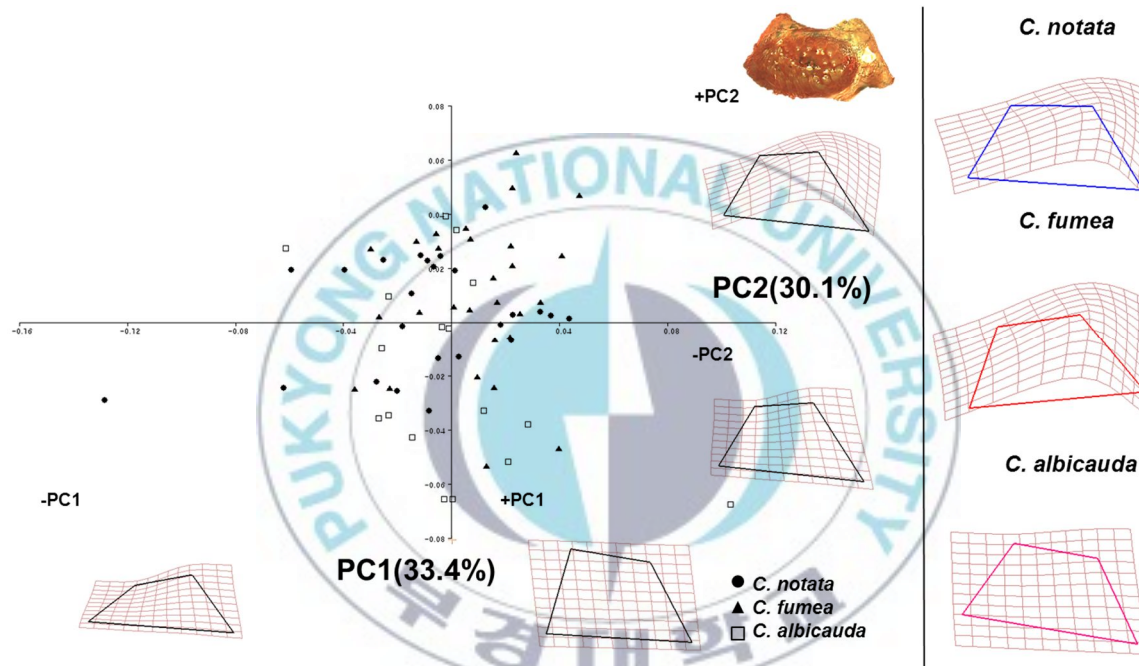


Fig. 13 Scatter plot of principal score 1 and 2 (PC1 and PC2) of the Upper pharyngeal jaw. Morphologika2 Deformation grids indicate shape variation represented by PC1 and PC2 (minimal (-PC) and maximal (+PC) values).

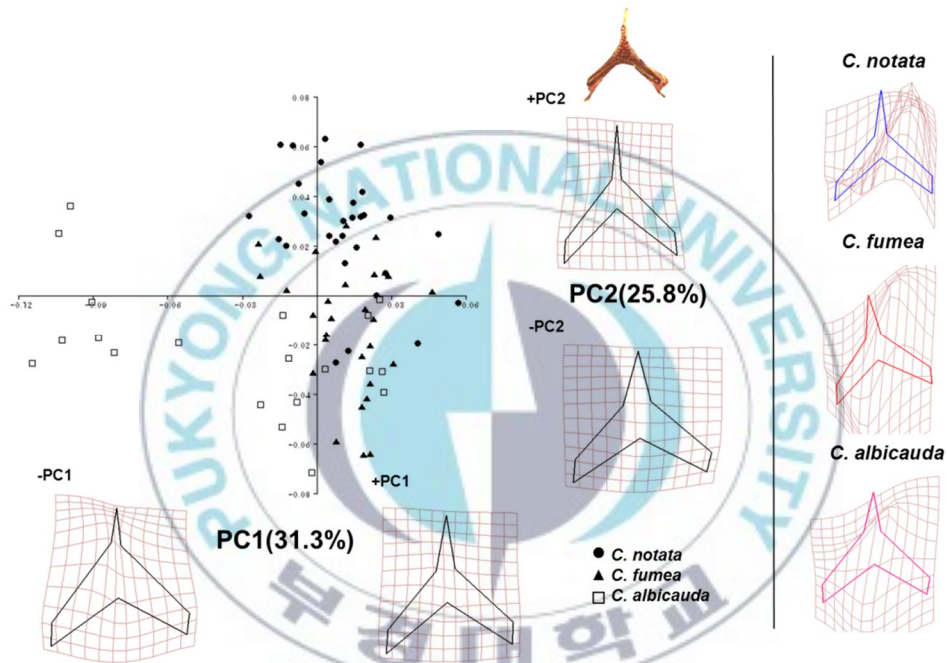


Fig. 14 Scatter plot of principal score 1 and 2 (PC1 and PC2) of the Lower pharyngeal jaw. Morphologika2 Deformation grids indicate shape variation represented by PC1 and PC2 (minimal (-PC) and maximal (+PC) values).

ii. CVA

The ordination of groups by canonical variate analysis corroborated the findings that shape differences were significant between groups. The discrimination between groups could be also interpreted by examining the ordination of specimens in the morphospace defined by the CV axes (Figs. 15–20). Generally, the results could expand the interpretation of the previous description or shown the same features of the principal component analysis results.

For the premaxilla, all species were clearly separated in this shape space. The axis CV1 (81.6%) distinguished two groups: *C. notata* group and *C. fumea* group. *C. albicauda* was distinguished by the axis CV2 (Fig. 15). For the maxilla, the axis CV1 indicated 67.3% of the total variation, and it separated two groups. *C. notata* and *C. fumea* were distinguished according to the axis CV2 (32.7%) (Fig. 16). Concerning the dentary, the CV1 and CV2 axes clearly individualized each species (Fig. 17). The axis CV1 allowed the clear distinction of *C. notata* and *C. fumea* by 77.1% of the total variation. *C. albicauda* was distinguished by the axis CV2. For the angular and retroarticular, the results showed the clear division of three species. Along CV2, *C. notata* and *C. fumea* were separated in this shape space. *C. albicauda* was distinguished by the axis CV1 (Fig. 18). For the upper pharyngeal jaw, all species concentrated one group in this shape space (Fig. 19). Concerning the lower pharyngeal jaw, all species were separated in this space unclearly but *C. albicauda* was located in space far away from two species (Fig. 20).

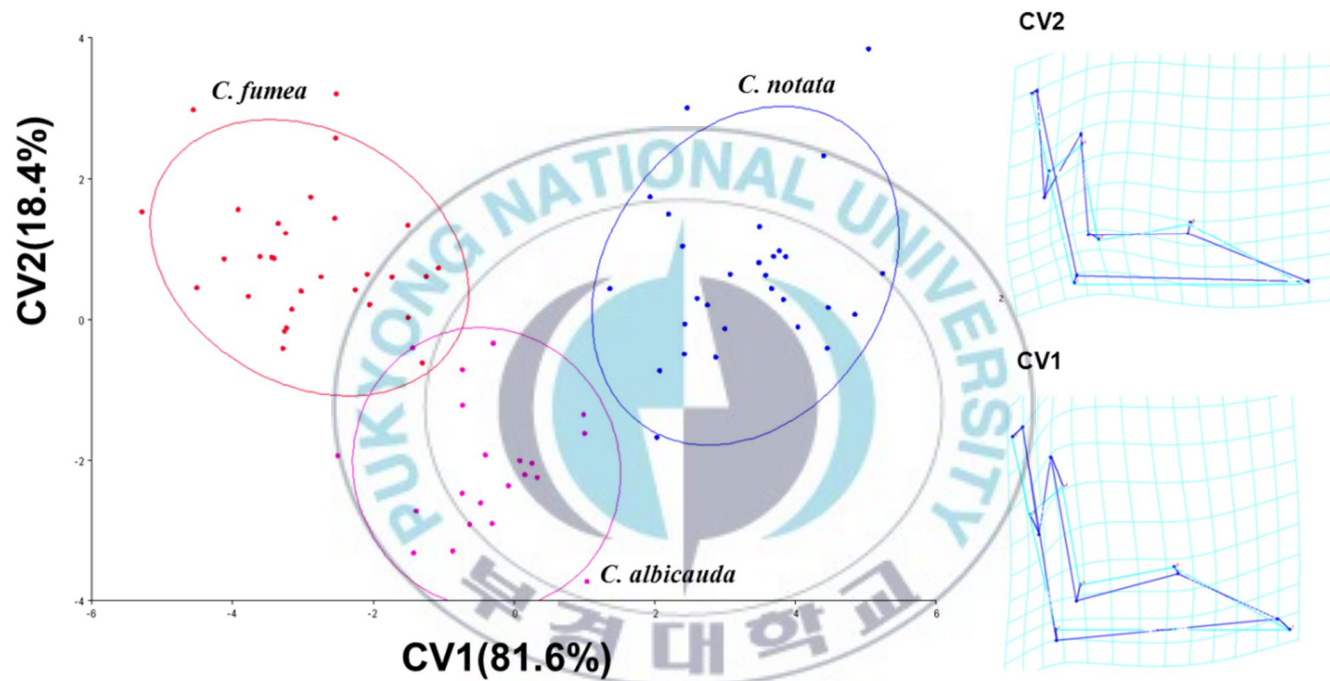


Fig. 15 CVA ordination for the Premaxilla between three species. The combination of the transformation grid and wireframe graph (on the right) along the first two CV axes using the Morpho J program.

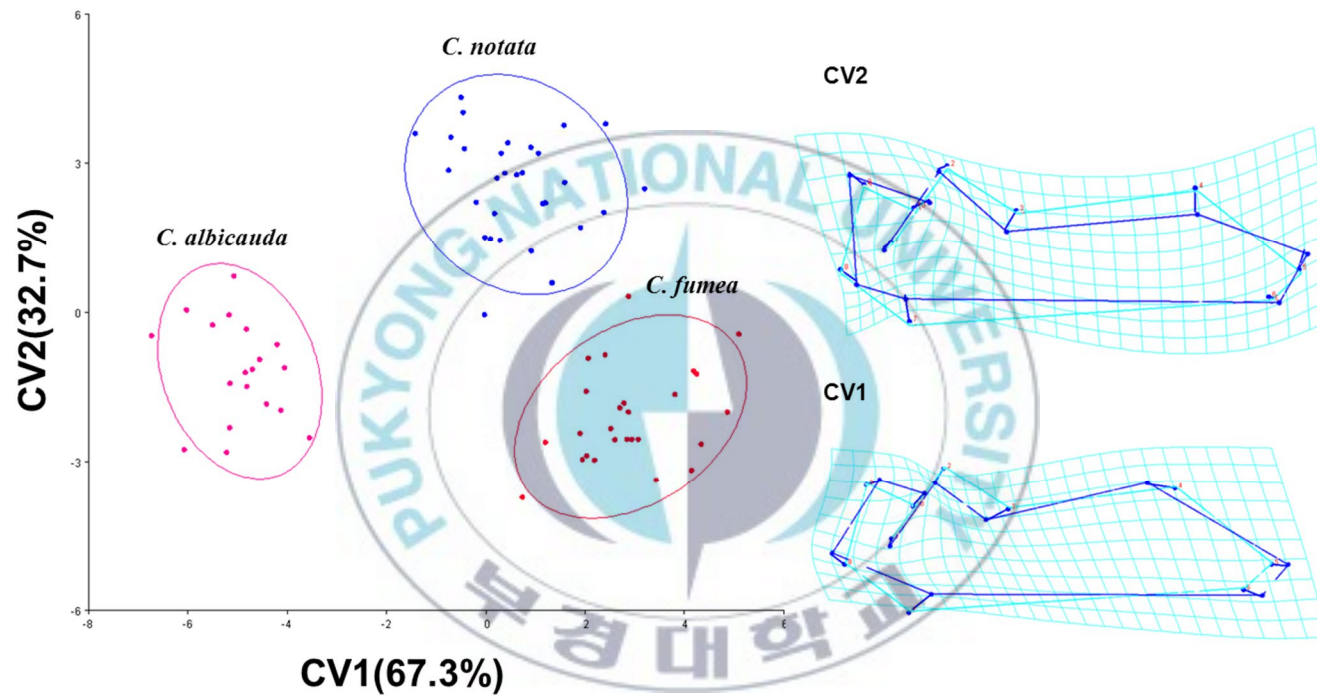


Fig. 16 CVA ordination for the Maxilla between three species. The combination of the transformation grid and wireframe graph (on the right) along the first two CV axes using the Morpho J program.

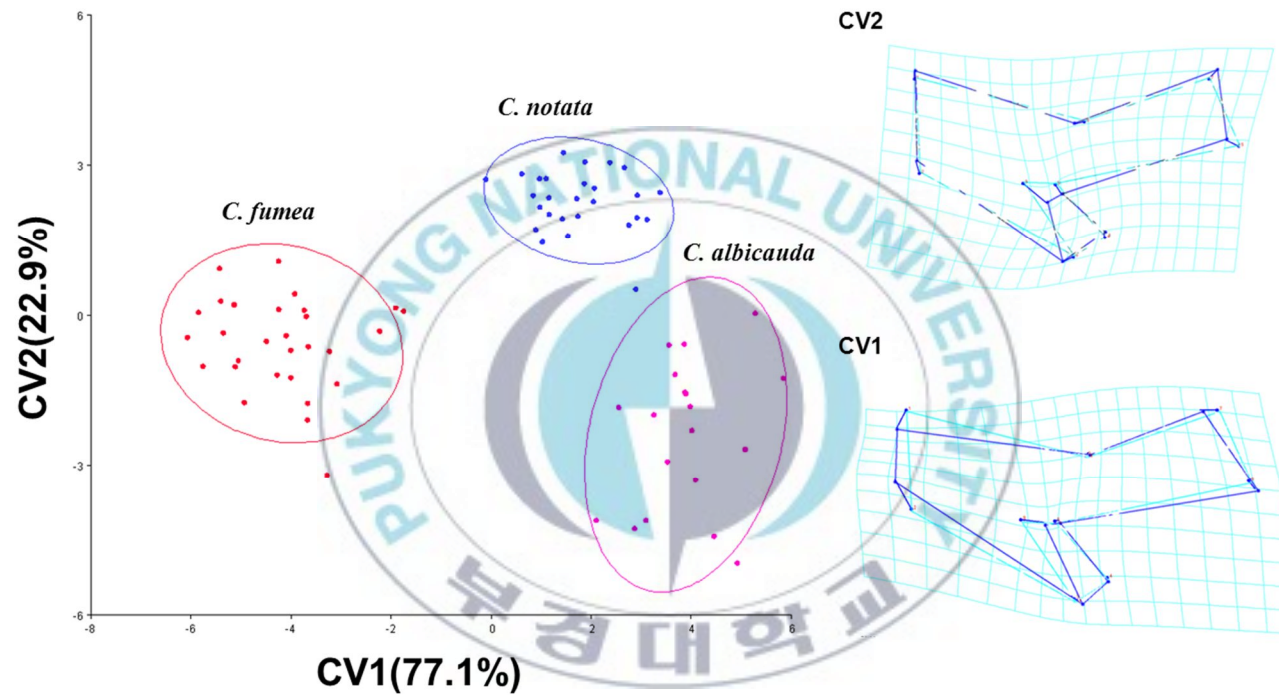


Fig. 17 CVA ordination for the Dentary between three species. The combination of the transformation grid and wireframe graph (on the right) along the first two CV axes using the Morpho J program.

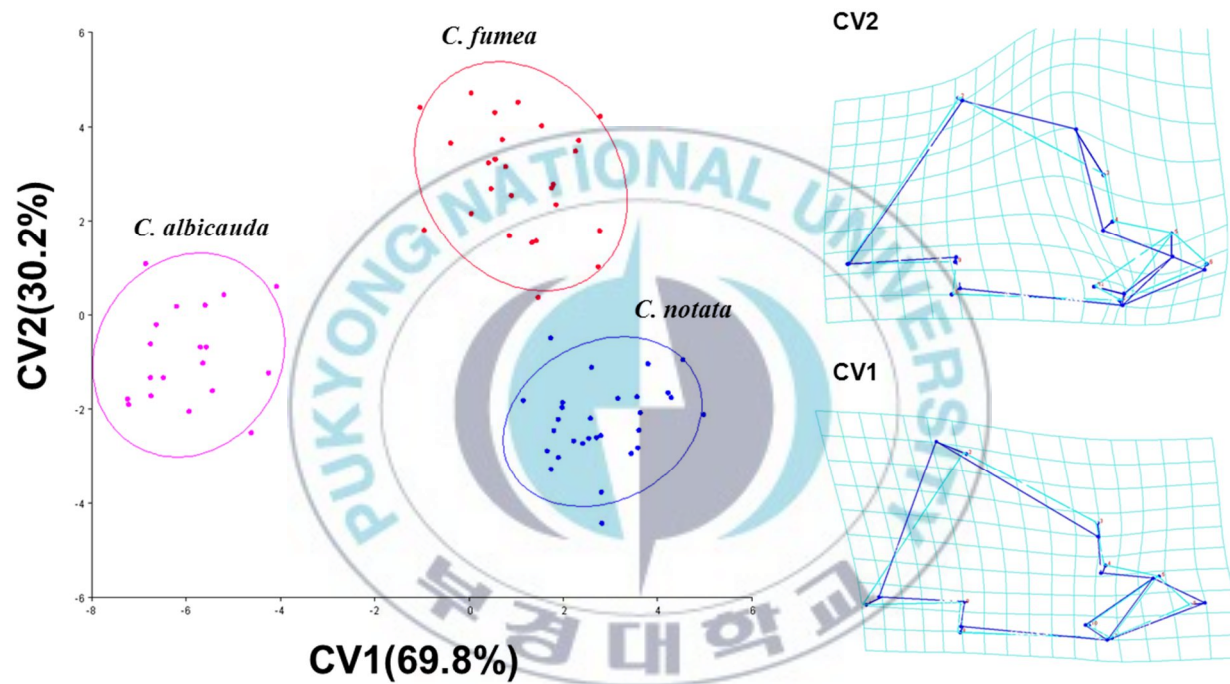


Fig. 18 CVA ordination for the Angular and retroarticular between three species. The combination of the transformation grid and wireframe graph (on the right) along the first two CV axes using the Morpho J program.

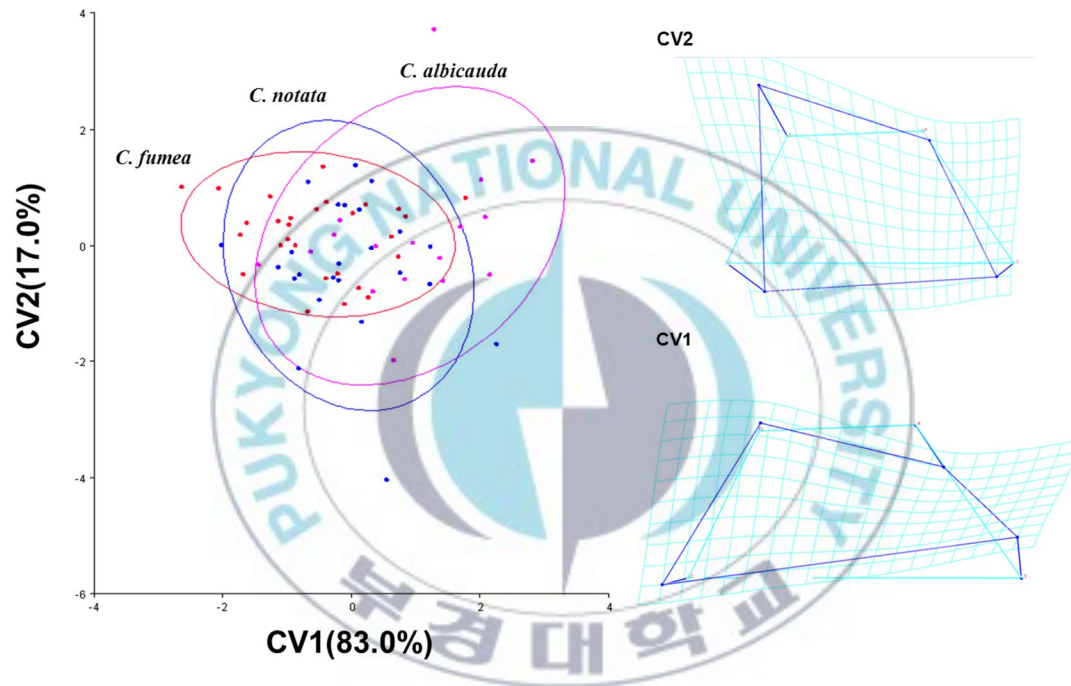


Fig. 19 CVA ordination for the Upper pharyngeal jaw between three species. The combination of the transformation grid and wireframe graph (on the right) along the first two CV axes using the Morpho J program.

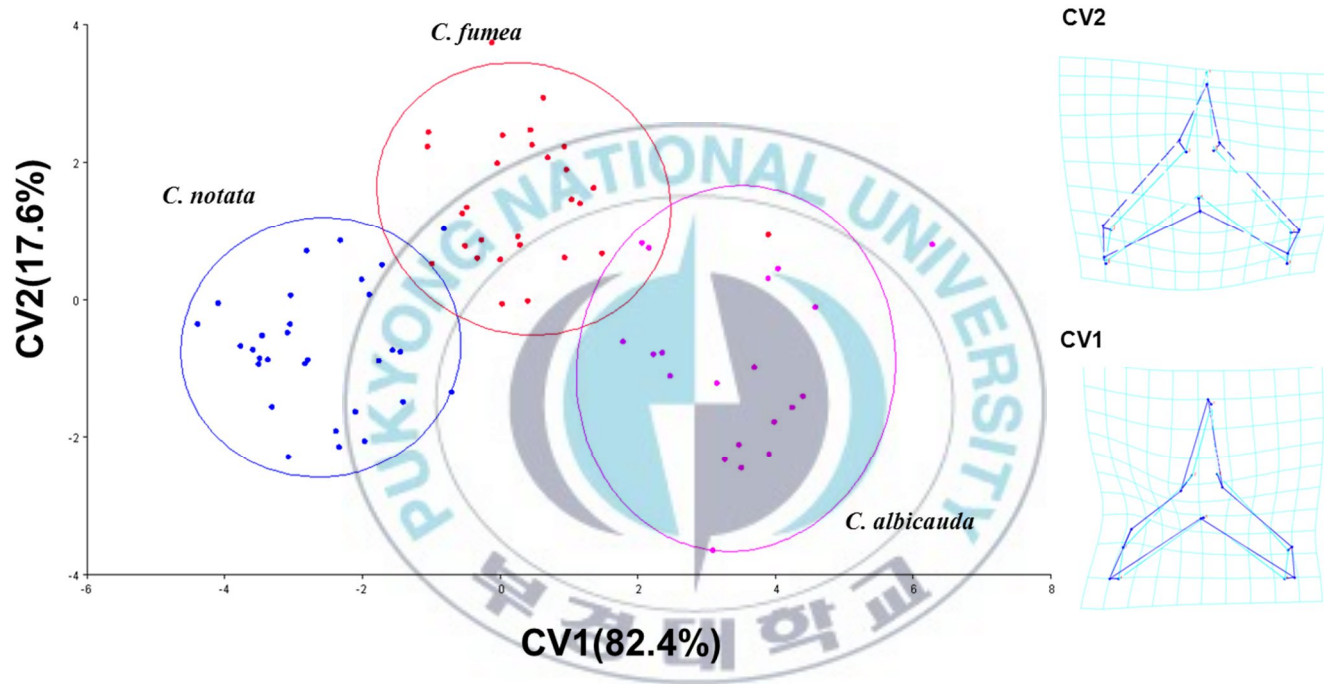


Fig. 20 CVA ordination for the Lower pharyngeal jaw between three species. The combination of the transformation grid and wireframe graph (on the right) along the first two CV axes using the Morpho J program.

IV. Discussion

1. Relationship of jaw shape and feeding methods

i. Jaw shape and function

A morpho-functional analysis in trophic aspect is used for an important method to study the iterative evolutionary radiation system of damselfishes (Frederich et al., 2008; Frederich and Vandewalle, 2011). The differences between the morphological characters are normally translated by variations in the performance of the organisms achieving a definite task (Wainwright and Richard, 1995). In the study of skeletal characters for three species of genus *Chromis* (*C. notata*, *C. fumea*, and *C. analis*) by Kim and Kim (1997) mentioned that *C. notata* and *C. fumea* are different from the jaw skeletal shape. In the present study, the jaw skeletal morphology between three species clearly verified a definite difference by using landmarks in geometric morphometric analysis. Three species (*C. notata*, *C. fumea* and *C. albicauda*) are distinctly distinguished by the shape of premaxilla, dentary, and angular and retroarticular among five skeletal units.

The premaxilla, which is the main bone of the upper jaw, is closely related to the successful evolution of the teleost fishes (Alexander, 1967), and the ability of protrusion of upper jaw enhanced by a long ascending process of the premaxilla (Gosline, 1987). In the present study, *C. fumea* seems to be more developed the protrusion of upper jaw than *C. notata* because of the various characters based on

the long and narrow ascending process and the deeper groove between dentigeorus process and ascending process. In addition, because the angle size ($^{\circ}$) between ascending process and angular process can decrease the distance between predator and prey, these advantages may be ultimately lead to the increased prey capture success (Barel, 1983; Coughlin and Strickler, 1990; Liem, 1993; Staab et al., 2011). Especially, The relatively long and narrow ascending process and the deeper groove between dentigeorus process and ascending process increase the protrusion of upper jaw by bordering the muscles attached region and these are the highly adapted shape aspects of the protrusion (Otten, 1983; Kim and Kim, 1997).

The helical joint region of lateral process is related to the smooth moving of upper jaw and help to protrusion of upper jaw together with the premaxilla (Liem and Osse, 1975). Most of genus *Chromis* species are known as feeders to suck zooplankton (Randall, 1967). However, in the aspect of functional shape of upper jaw, *C. notata* was considered as being adapted shape to feed more non-active prey than *C. fumea*. *C. albicauda* seem to the benthic feeder based on the most developed joint region of the lateral process of maxilla. In case of *Oryzias javanicus* having the non-protrusible shape of the jaw, they have an adapted shape for feeding non-activity prey such as organic and/or detritus in the water rather than sucking an activity prey (Mok and Munro, 1991).

In the dentary shape, the long ventral region of the dentary ($\hat{=}$ Symphysis of mandible) is the major functional character of grazer in particular (Barel, 1983; Kassam et al., 2004). Also, the thick and short mandible have been well adapted to provide stable force when feeding the prey such as algae and benthic organism

(Liem, 1993; Wainwright and Richard, 1995). *C. notata* was provided to stable force relatively now that they have the higher and shorter mandible than *C. fumea*. According to the Weaver (2001), the feeding of the hard-bodied prey such as crustaceans brings to increase the number of teeth and the height/thickness of lower jaw. And Genus *Epinephelus* species in Serranidae prevent the jaw from distortion by providing a greater bite force from the thick mandible when feeding the hard-prey (Weaver, 2001). That suggests the possibility that *C. notata* may be feeding on hard-prey slightly based on thick mandible shape. Whereas, the mandible in *C. fumea* could be also lead to the increased velocity of jaw opening due to the reduction of overall bone mass. And these results are regarded as functional traits to feed on the prey having a high swimming ability such as copepods. The thickness of the lower jaw and density/size of teeth brings to the differences of the prey between species, in addition, these affect to the prey capture ability (Weaver, 2001). All of three species share the conical-form teeth, but the teeth size and number of *C. notata* indicate the high within-species variation.

The upper and lower pharyngeal jaw mainly performs to the function to help prey to adjust and swallow, and their shape appears to the high variation between taxonomic groups (Lauder, 1983). Three species were very developed their pharyngeal jaw because they immediately swallow the incoming prey through the oral cavity without chewing. The thin and sharp teeth in several rows on their dentigeorus process were regarded to help a little-hard prey to break into little pieces. That was regarded as the functional shape of zooplankton feeder. *C. abicauda* had the broader dentigeorus process than the others. Especially, the

pharyngeal jaws could perform an important role in cichlid speciation in general (Muschick et al., 2011). The Labroidei including Labridae, Pomacentridae, Scaridae and Embiotocidae is originally hypothesized about the monophyly because of the similar pharyngeal jaws but, Mabuchi et al. (2007) suggested again the polyphyly because the pharyngeal jaws of Labridae and Pomacentridae was formed a single fusion skeletal unit (Liem, 1986; Stiassny and Jensen 1987; Helsey, 2006; Mabuchi et al., 2007). The large body and benthic fishes mainly possess the broad dentigeorus process shape and are more remarkable molariform jaw type (Muschick et al., 2011). For example, the exercise aspect of the pharyngeal jaw in Embiotocidae is crashing like as zigzag the upper and lower teeth each other, and then the prey was broken secondly (Liem, 1986). In Baikal Cottoidei (*Paracottus knerii*, *Leocottus kesslerii*, and *Batrachocottus baicalensis*), the upper pharyngeal jaw teeth has in the functional role to seizing the prey and then pushing into the pharynx. And the lower pharyngeal jaw teeth are directed toward the pharynx, which prevents the prey to move forward again (Tolmacheva, 2010). The upper pharyngeal jaw of *C. notata*, *C. fumea* and *C. albicauda* possessed the teeth both conical and canine form of conspicuous shape. The teeth of various forms and dentitions are closely related to diet, feeding methods and jaw shape in fishes (Gosline, 1985; Liem, 1993; Westneat, 1994; Wainwright and Richard, 1995; Wainwright and Bellwood, 2002).

The gill rakers of *C. notata* and *C. fumea* have the narrow interspace of gill rakers and a lot of numbers. The shape of gill rakers, which are important character in feeding, limits on the ability to retain the zooplankton of certain sizes in fishes (Wright et al., 1983; Link and Hoff, 1998; Lipsey and Stockwell, 2001;

Budy and Haddix, 2005). And the number of gill rakers has a central role in determining the foraging ability towards zooplankton prey (Kahilainen et al., 2011). So, three species seem to be adapting morphology to feed on zooplankton efficiently. In addition, the gut morphology often reflect to the environment of feeding habitat (Randall, 1967). The diverse trophic ecology in angelfishes appears better explained the gut morphology than by skull morphological disparity (Konow and Bellwood, 2011). Also, feeding apparatus is related to various elements composing the structure. For example, the amount of muscles affect to increase their feeding ability in fish (Frederich et al., 2008). Besides, planktonic feeder often has a skull shaped to improve the design of the cone consisting of a high suspensoria and opercles and a high supraoccipital crest, and they can increase the insertion of a well-developed epaxial muscle mass responsible for the rise of the neurocranium during mouth opening (Liem, 1993; Frederich et al., 2008).

In the present study results, some of the results suggested that *C. notata*, *C. fumea*, and *C. albicauda* are the highest level of planktonic feeder. The premaxilla, dentary and angular and retroarticular were clearly significant differences, but the maxilla, upper and lower pharyngeal jaw was no significant differences between species. In the morphometric analysis, the result of each skeletal units discordance could be explained to the several factors in the responsibility for this incongruence. Frederich et al. (2012) explained the four reasons: an incomplete assessment of the information according to the different landmark set criteria each bone, a different functional demands of each skeletal unit, the number of elements composing the structure, and the number of genetic factors underlying

morphological differences.

This study suggested that the difference and variation of jaw skeletal structure could be associated with diet transition, feeding behavior and the functional morphology of the other organ.



ii. Feeding methods

The differences in prey capture ability by feeding apparatus (i.e., Oral and pharyngeal jaws and their associated teeth, etc.) and feeding activity between three species may be related to the diet characters and dietary transition. *C. notata* showed that the protrusion ability of the upper jaw was slightly lower than *C. fumea* because of the shorter ascending process of premaxilla and the larger angle between ascending process and angular process of premaxilla. And the thick and short mandible was the adapted morphology to feed on hard-prey. Whereas, *C. fumea* had the long ascending process and the small angle size between ascending process and angular process, and these characters showed that their protrusion ability was more developed than *C. notata*. The thinner and proportionally longer mandible (i.e. The short ventral region of dentary) of *C. fumea* possessed the well adapted morphology to hold and capture an activity prey such as pelagic zooplankton rather than chewing the prey. Although the maxilla, upper and lower pharyngeal jaw were not founded definite differences between species, the external shape in *C. notata* and *C. fumea* was slightly different. All possessed the advantageous morphology of zooplankton feeder. *C. albicauda* possessed the expanded joint region of the lateral process of maxilla and the broader dentigeorus process of the lower pharyngeal jaw than the others. It was considered that *C. albicauda* might be benthic feeder. Specifically, premaxilla of *C. albicauda* was similar to *C. notata*, but the dentary was similar to *C. fumea*.

In fishes, to clarifying the interspecific difference in the prey organism in relation to body shape variations is fundamental aspect in understanding the

feeding ecology of fishes and furthermore, estimating the evolution radiation mechanism (Nanami and Shimose, 2012; Frederich et al., 2013). In general, teleosts capture the prey by using water column transportation and then transfer prey to oral cavity by sucking (Lauder, 1983). Numerous previous studies have shown that body shape variation effects on the feeding behavior in fishes (Webb, 1984; Walker, 1997; Wainwright and Bellwood, 2002; Svanback and Eklov, 2003; Case et al., 2008). The damselfishes commonly recognized three trophic groups/prey capture methods: pelagic feeders (Ram and/or Suction feeding), benthic feeders (Grazing algae or biting coral polyps), Intermediate group (feeding on planktonic prey, small benthic invertebrates, and algae) (Allen, 1991; Cooper and Westneat, 2009; Frederich, 2013). Most of the coral reef fishes use the grazing or scraping feeding methods (Wainwright and Bellwood, 2002). Genus *Chromis* species are known as pelagic feeder, which is catching a variable amount of the zooplankton (Frederich et al., 2013). Squamipinnes fishes are main biting group: Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes), Acanthuridae (surgeonfishes), Siganidae (rabbitfishes) (Tyler and Sorbini, 1999). Most of the wrasses fishes select the grazing/biting methods to grab-and-tearing the algae or the coral (Konow et al., 2008).

However, some species use the ram and suction feeding methods during the capture of mid-water prey. In wrasses, suction feeding is also an important role in feed on the attached and benthic prey (Ferry-Graham et al., 2002). Genus *Plectroglyphidodon* and *Stegastes*, in Pomacentridae, mostly feed on algae and corals using grazing or biting methods (Randall, 1967). The species of barracudas, which is known as rapid ram-feeding striker, are adapted to be less affected by the

prey size when opening the mouth because they have a sharp teeth and the strong jaws like as scissors to cut large prey into pieces (Grubich et al., 2008).

The morphological variation of the premaxilla and mandible structure is closely related to the tropical evolutionary of damselfishes (Frederich et al., 2008; Cooper and Westneat, 2009; Frederich and Vandewalle, 2011). Frederich et al. (2009) analyzed the stomach contents for thirteen sympatric species of damselfishes, which live in the Grand Recif of Toliara, Madagascar, and it reveals that their trophic niche is related to feeding character. Most of the genus *Abudefduf* species have a tricuspid tooth form, which mainly appears to the herbivorous fishes, for example, the prey organism of *A. saxatilis* is mainly comprised of over 50% of the algae and the corals (Randall, 1967). The stomach contents of *Microspathodon chrysurus*, which is one of the most common fishes of coral reefs in the West Indies, were observed feeding on over 90% the algae and organic detritus, that is never fed on planktonic organisms (Randall, 1967). *Chromis cyanea* and *C. multilineata* appear to feed only on the smaller zooplankton (over 50% of copepods), and their feeding behavior is the jaws snapping rapidly outward during feeding. It has a large correlation between the ecology information (I. e. Habitat or feeding region) and main prey organism so we can infer easily about it. Three species (*C. notata*, *C. fumea*, *C. albicauda*) feed mainly on copepods (Allen and Erdmann, 2012). And the result of this study suggested that the they were adapted in the different feeding method (i.e., grazing feeding, suction feeding/ram feeding in *C. notata* and suction/ram feeding in *C. fumea*). Frederich et al. (2012) suggested that the morphological change of jaw skeleton may be affected by various trophic factors such as feeding competition or feed availability. In

Pomacentridae, the differences of diet according to the change of prey capture ability, lead to the morphological modification of the feeding apparatus and/or the change of feeding activity (Kotrschal, 1988; 1989). Also, its differences could may be related to the ecology and genetic factors.



2. Adaptation aspects during evolution

The aim of ecomorphological method is to reveal and understand the interaction between fish morphology and ecological factor (Norton et al., 1995). According to Ferry-Graham et al. (2002) and Cooper and Westneat (2009), ecomorphological approach method have already been used to study ecological/morphological structure, distribution, evolution and the trophic relation. In pomacentridae, Tang (2001) revealed the discrepancy between the morphology and molecular phylogeny. The previous morphology classification was reviewed by many researchers (Jang-Liaw et al., 2002; Quenouille et al., 2004; Cooper et al., 2009). Recently, according to Frederich et al. (2012), *Pomacentrus coelestis* appeared the difference in mandible shape between mainland Japan and Okinawa-Taiwan. The results were well matched to the result of the genetic differences. According to Randall et al. (1981), *C. notata* was changed frequently along with the collected region. In Korea, the pectoral fin base of *C. notata* tended to be changed the spot shape of that in Jeju-do to go northwards. The previous study that the separation of the body shape, dentition type and jaw-lever mechanics of the four lutjanid species (*Lutjanus decussatus*, *L. fulvivflamma*, *L. fulvus* and *L. gibbous*) in the same habitat, was occurred via the evolution, and it followed the difference with prey partition or prey preference, and it was one of the reasons why they could coexist without the prey-competition (Nanami and Shimose, 2012).

In present study, *C. notata* and *C. fumea*, and *C. albicauda* lived in the same habitat, but seemed to avoid the interspecific competition by varying their trophic/ecological niche. To support the results is that *C. notata* were superior in

numbers than *C. fumea* and *C. albicauda* in comparison with the fishery amount was caught by lift net at a time. In the character that *C. fumea* and *C. albicauda* frequently occur in tropical and subtropical seas, the living individuals in Jeju-do appeared to the lower frequency occurrence than *C. notata*. And these results were considered by varying their ecological niche. The factor of different trophic-ecological niche could be the difference of prey selectivity and environmental effect such as the habitat depth and water temperature. According to Frederich et al. (2008), the result of the molecular phylogeny in pomacentridae corresponded with the phenotypic relationship of mandible and premaxilla. So, we suggested that the shape of jaw structure can be closely related to the evolutionary character. And also, in the relationship between feeding method, which was inferred from the jaw shape, and the molecular phylogenetic result, the ancestral species was considered to herbivorous feeders such as *Stegastes*, *Plectroglyphidodon* species, and the jaw morphology of the pelagic feeder (i.e. Genus *Chromis*) and the omnivorous feeder (i.e. Genus *Dascyllus*) and the occurrence of two feeders shown that damselfishes have been undergoing two times of changes during the evolution by adapting to avoid the prey competition in the limited coral reef habitat environment (Frederich et al., 2008).

In this study, *C. notata* and *C. fumea* mainly act as pelagic feeder, which feed on zooplankton. However, they seem to be adapted in feeding method such as grazer with the result of *C. notata* jaw morphology. Whereas, *C. fumea* is regarded as typical suction feeder using ram/suction. Recently, according to the molecular results, *C. notata* was more recently specialized but it was more similar to the ancestral morphology (Frederich et al., 2013). When associating with previous

studies by Frederich et al. (2008), the jaw shape of *C. notata* may be similar to the jaw shape of herbivorous fish. It is a very important result to understand the difference with jaw morphology among three species.

C. notata was well adapted to temporal and polar waters than *C. fumea* and *C. albicauda* in that *C. notata* only existed in Jeju-do in time past, but recently they occur in Dok-do (deep depth and low water temperate). Also, in the worldwide, the distribution of three species presented the significant difference that *C. notata* had a relatively limited distribution, including Taiwan, China, Ryukyu Islands, Southern Japan, whereas *C. fumea* and *C. albicauda* widely distributed in Indo-West Pacific, eastern edge of the Indian Ocean, Australia, etc. In other wards, some of the jaw shape differences between the three species were considered as the differently adapted shape during evolution. The dietary transition in fishes might affect the number of teeth and the shape of the jaws and/or pharyngeal jaws.

Furthermore, in this study, if it reveals definitely the evolutionary history of genus *Chromis* species, we have to examine and to analyze diet in detail. Today, many studies of pomacentridae were still proceeding in worldwide, but lack in Korea. Thus, it needs to discuss and study more various studies in morphology, molecular phylogenetics, and genetic population studies in the various subtropical species such as angelfishes, butterflyfishes, etc.

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먼저, 바쁘신 중에도 소중한 시간을 내주시어 꼼꼼하게 논문을 검토해주시고, 완성도 높은 논문이 될 수 있도록 조언해주신 박원규 교수님과 김병직 박사님께 깊은 감사의 말씀드립니다. 학부생 때부터 대학원에 진학하여 지금에 이르기까지 열정적으로 학문을 가르쳐주신 김수암 교수님, 남기완 교수님, 오철웅 교수님, 백혜자 교수님, 박원규 교수님, 김현우 교수님께 감사드립니다.

이제는 가족이 되어버린 저의 버팀목이자 활력소였던 어류학실험실은 정말 평생 잊지 못할 추억만 가득 남겨주셔서 행복하게 학위 과정을 마무리할 수 있었습니다. 늘 한결 같이 밝은 미소와 따뜻한 말씀으로 저를 대해주신 유정화 박사님, 학문적인 부분으로 많은 도움을 주신 박경동 박사님, 든든한 선배님이신 반태우 선배님, 학문에 대한 상담과 인생상담 모두 잘 해주시는 박정호 선배님, 유머와 재치로 실험실 분위기를 이끌었던 정용태 오빠, 비록 짧은 시간이었지만 따뜻하게 챙겨주었던 김은아 언니, 없으면 정말 허전하고 빈자리가 크게 느껴지는 엄마 같은 언니 권내림 언니, 박꽃님 언니, 멀리 떨어져있어도 항상 먼저 챙겨주는 고마운 김유미 언니, 똑순이가 어울리는 최은정 언니, 항상 상대방을 먼저 생각해주던 남윤주 언니, 정말 잘 챙겨주셨던 정문경 언니 모두 감사의 말씀드립니다. 또한, 톡톡튀는 유머로 늘 웃음을 주시는 지환성 오빠, 당근과 채찍을 끊임없이 주었던 권혁준 오빠, 지금까지도 어류학실험실의 든든한 방장 이수정 오빠, 학부생 때부터 지금까지 옆에서 한결같이 힘이 되어준 소중한 친구 배승은양, 도움이 필요할 때 언제나 자기 일처럼 열심히 도와준 어방의 김수현 명세훈 오빠, 활력넘치는 에너지와 재치를 겸비한 사진작가 유효재 오빠, 귀여운

매력을 가진 이우준 오빠, 4차원적 매력이 넘치는 한상윤 오빠, 나이는 어리지만 든든한 오빠 같은 장인철군, 마음씨가 너무 고운 어방의 막내 귀염둥이 장서하양, 윤희지양까지 지금의 어류학 실험실원들에게도 모두 감사드립니다. 학부와 대학원 생활동안 근처에서 묵묵히 든든한 지원군이 되어주었던 모든 분들께 감사드리며 먼저, 같이 행복한 시절을 함께 하고 7년 동안의 소중한 추억들을 함께 간직하고 있는 오랜 친구 사이 최은혜, 허운영, 안지혜, 김성희, 박다정 모두 항상 응원해주어서 정말 고맙고 사랑합니다. 나에게 근사한 화분을 선물해 준 장미같은 김정연양, 항상 웃는 얼굴로 대해 주던 든든한 김대근 오빠, 행복한 모습이 보기좋은 김효은양, 신아리양, 2층에 가면 항상 밝은 얼굴로 맞이해 준 따뜻한 친구 사이 김아란양과 이지현양, 비전공분야에도 전하면서 정말 많은 도움주었던 박주은, 전유진양, 학부때부터 늘 잘 챙겨주셨던 조혜정언니, 똑똑이 김아름양에게도 고마운 마음을 전합니다. 바쁘단 이유로 자주 보지 못해서 늘 미안하고 고마운 세상에 둘도 없는 나의 사랑하는 고향 친구들 우리 큐(Q) 신가은, 임보람, 문세인, 정하나, 그리고 진아란, 정혜란, 김은비, 김효정양, 서준호 오빠, 룸메이트 최수진양까지 모두 끝까지 지켜봐주고 응원해주셔서 감사합니다.

마지막으로, 26년동안 저를 믿고 묵묵히 지원해주시느라 고생하신 사랑하는 나의 부모님께 감사의 마음을 전하며, 제가 옳고 그름을 잘 판단할 수 있도록 고민과 인생진로 상담 잘해주던 사랑하는 쌍둥이언니, 남들과 달리 조금은 몸이 불편하지만 언제나 씩씩하고 밝은 우리 남동생 명찬이, 늦둥이로 태어나 이제 중학교에 입학하는 우리집 귀염둥이 막내 유나까지 모두 깊은 감사의 말씀드립니다.