# DESCRIPTIVE AND COMPARATIVE STUDY OF AGONISTIC BEHAVIOR AMONG SIX SPECIES OF ANABANTID FISHES: GENUS ANABAS, SANDELIA, AND CTENOPOMA

By

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# DESCRIPTIVE AND COMPARATIVE STUDY OF AGONISTIC BEHAVIOR AMONG SIX SPECIES OF ANABANTID FISHES: GENUS *ANABAS*, *SANDELIA*, AND *CTENOPOMA*

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# CHAPTER I

# INTRODUCTION

A large group of perch-like fishes distributed through much of southern Africa and Asia comprise the suborder Anabantoidei. Most Anabantoids are relatively small and tend to inhabit shallow lakes and ponds or sluggish streams and weedy backwaters of larger rivers. Many of the Asian species inhabit temporary waters or shallow, stagnant pools that have relatively low oxygen content. The principle adaptation that has permitted anabantoids to utilize these inhospitable, but often abundant, habitats is a unique suprabranchial respiratory apparatus that permits them to obtain oxygen by gulping air at the surface. While many species are obligate air gulpers, surfacing periodically even while inhabiting richly oxygenated water (Miller, pers. comm.), others surface less frequently, and fishes of the Genus *Sandelia* have, apparently secondarily, dispensed with aerial respiration in their high-oxygen upland streams. Most evolutionary lines, however, continue to take advantage of this primary adaptation, and consequently have had many aspects of their behavior and biology constrained by it. For example, most Asian species, and one group (see below) of African species has independently evolved bubblenest blowing behavior, which produces a floating nest for fertilized eggs. A large suite of behaviors that serve to optimize this strategy is strikingly obvious and has been utilized by Miller and Robison (1974) and Miller and Jearld (1983) to hypothesize phylogenetic relationships among species in two Asian genera. To date, however, the only comprehensive phylogenetic analysis of the entire suborder is Liem's (1963) now outdated and incomplete osteological study.

Liem (1963) placed three of the Asian families in one clade (Fig. 1), and members of the Family Anabantidae were divided into two lines. He separated the African Genera, *Ctenopoma* and *Sandelia*, from the Asian Genus *Anabas*, and hypothesized that the family had originated in Asia and migrated (in part) to Africa. Although no one has yet attempted a comprehensive systematic revision of the Asian forms, Norris (1987) recently completed a revision of the Genus *Ctenopoma*, and included suggestions on the phylogeny of the Family Anabantidae (Fig. 2). Norris (pers. comm.) is presently conducting an osteological analysis of the group and is extending his earlier studies to several previously unnamed forms from Central Africa. The present study is part of an N.S.F. sponsored project to compare behavioral and morphological data on phylogenetic relationships of the group.

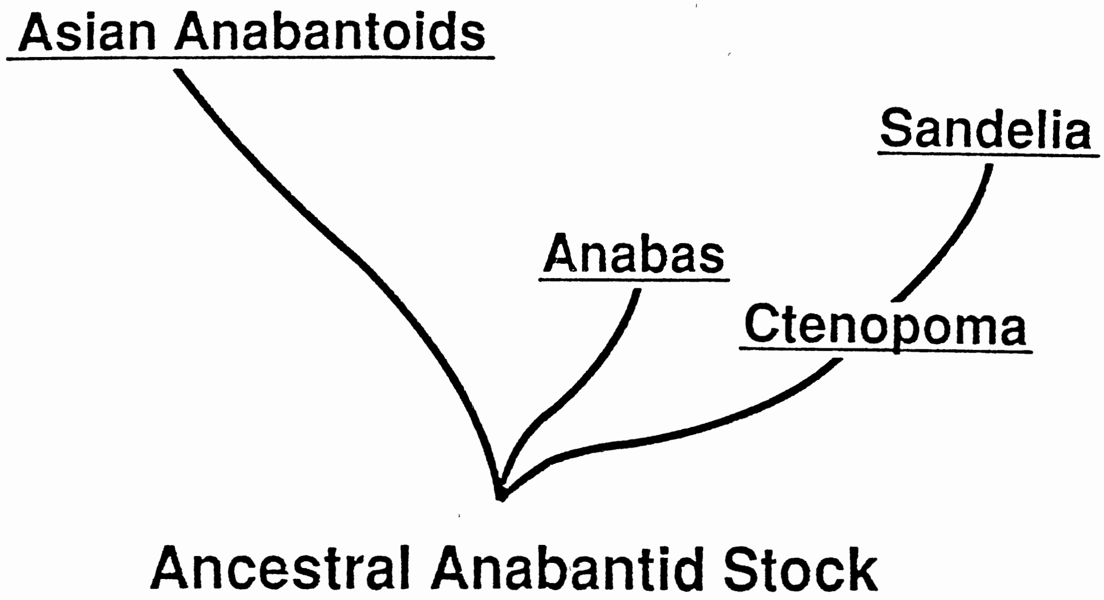


Figure 1. Anabantid phylogeny presented by Liem (1963)

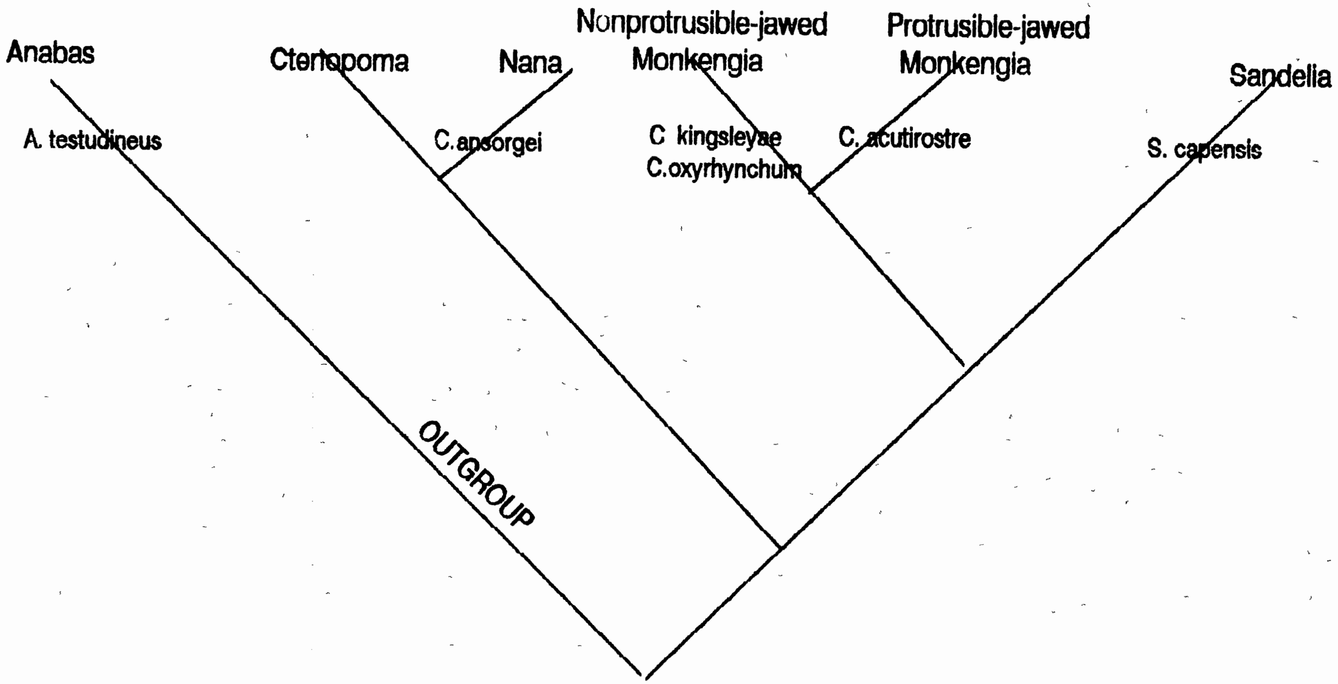


Figure 2. Phylogeny of Anabantidae presented by Norris (1987)

The early ethologists (Whitman, 1919; Tinbergen, 1951; Lorenz, 1941) had proposed that similarities in stereotyped behaviors reflected descent with modification among arrays of closely related species. Lorenz and his followers believed that these "instinctive" behaviors, by definition resistant to modification by learning during ontogeny, were as reliable indicators of phylogenetic relationships as morphological traits. Although Atz (1970) and others have questioned the validity of this view, it has persisted in mainstream ethology to the present (Ewing, 1975; Belcher, 1983; McLennan et. al., 1988). Miller and Robison (1974) and Miller and Jearld (1983) used frequency and duration of stereotyped acts occurring during courtship and spawning behavior to suggest phylogenetic relationships within the Asian Genera Trichogaster and Colisa, respectively. In general, behavior traits produced phylograms that were consistent with those suggested by morphological similarities. The facility with which these two groups lent themselves to a behavioral analysis may be due, at least in part, to the fact that there were only four species in each genus, and they appear to be closely related.

The Genus Ctenopoma, in contrast, consists of approximately 20 species assigned to three distinctive subgroups (Elsen, 1976; Norris, 1987) that exhibit far more morphological and behavioral variation than is seen in any of the Asian genera. If behavior can truly be used as an objective indicator of phylogeny, relationships among species of Ctenopoma, and among the Anabantid genera should be clarified by careful quantitative analysis of stereotyped behaviors. Because of the difficulty we have encountered in breeding these fish, we were forced to utilize agonistic behavior, rather than reproductive patterns, for this analysis. Although fighting behaviors have rarely been used in previous phylogenetic analysis, there seems to be no cogent reason for excluding this class of behaviors from such studies: they provide abundant, varied stereotyped acts that seem relatively independent of environmental influences (but see Tooker and Miller, 1980, for a detailed discussion of the ontogeny of agonistic behavior in a closely related Asian species). The present study, therefore, attempts to describe agonistic behaviors in four species in the Genus Ctenopoma (from two of the three subgroups) and compare these patterns with those exhibited by Sandelia capensis and Anabas testudineus. The phylogenetic hypothesis produced by examining similarities in fighting patterns will then be compared with the present system based on morphology.

# CHAPTER II

## MATERIALS AND METHODS

### Species Description

The six species studied are distinctive in appearance. C. kingsleyae is a deep bodied fish ranging up to 20 cm. SL, gray-brown with a greenish sheen and a dark caudal spot. C. acutirostre is the deepest bodied fish reaching a length of 15 cm. SL. The body is yellow-brown with numerous dark spots which extend into the fins. The head is pointed and the mouth is large. C. oxyrhynchum has a compressed deep body, reaching 10 cm. SL, reddish to greenish-brown with a large lateral dark spot. The caudal fin is clear with a black edge. These three species are members of a deep-bodied subgroup tentatively referred to under the proposed subgenus name Monkengia (Table I) by Norris (1987). C. ansorgei is a small elongate fish (60 mm. SL), brightly colored with 6-8 dark vertical bars and orange between the bars. C. ansorgei have long flowing striped dorsal and anal fins which are tipped in white. C. ansorgei is the only member of the Nana subgroup (Norris, 1987) observed in this study. S. capensis is a large fish (to 21 cm. SL) with a compressed elongate body and a large head and mouth. The olive to silver body has 8 black vertical bars which

## TABLE I

## SPECIES GROUPS OF CTENOPOMA

| Ctenopoma | Monkengia | Nana |
|---|---|---|
| *ashbysmithi* | *acutirostre* | *ansorgei* |
| *machadoi* | *kingsleyae* | *congicum* |
| *multispine* | *maculatum* | *damasi* |
| *nigropannosum* | *muriei* | *fasciolatum* |
| *pellegrini* | *ocellatum* | *intermedium* |
|  | *oxyrhynchum* | *nanum* |
|  | *petherici* |  |

Norris, 1987

change to an irregular mottled pattern, the black bars continue into the dorsal and anal fins. Pelvic fins are black with a white anterior edge. Three black bars radiate posteriorly from the eye over the opercle. A. testudineus has a deep body and large mouth and approaches 25 cm. SL. It is greenish dorsally with a yellowish belly, and has a black caudal spot and dark spot on the posterior edge of the opercle flap.

## Species Distribution

Goldstein (1971) and Pinter (1984) describe the distribution of A. testudineus as throughout Asia, frequently in polluted anoxic swamps and shallows (Fig. 3). Jubb (1967) and Norris (1987) describe the range of S. capensis as in the South Coastal drainage basin from the Langevlei River to the Coaega River of South Africa and in the mountain headwaters of many tributaries of those river systems (Fig. 4). Norris (1987) described the distribution of the Ctenopoma species studied (Fig. 4) as:

C. kingsleyae---Zaire basin and coastal drainages from Zaire to the Senegal River.

C. acutirostre--endemic to the Zaire River Basin throughout the cuvette centrale (forested area in the middle and lower reaches of the Zaire River Basin) and in the tributaries of the

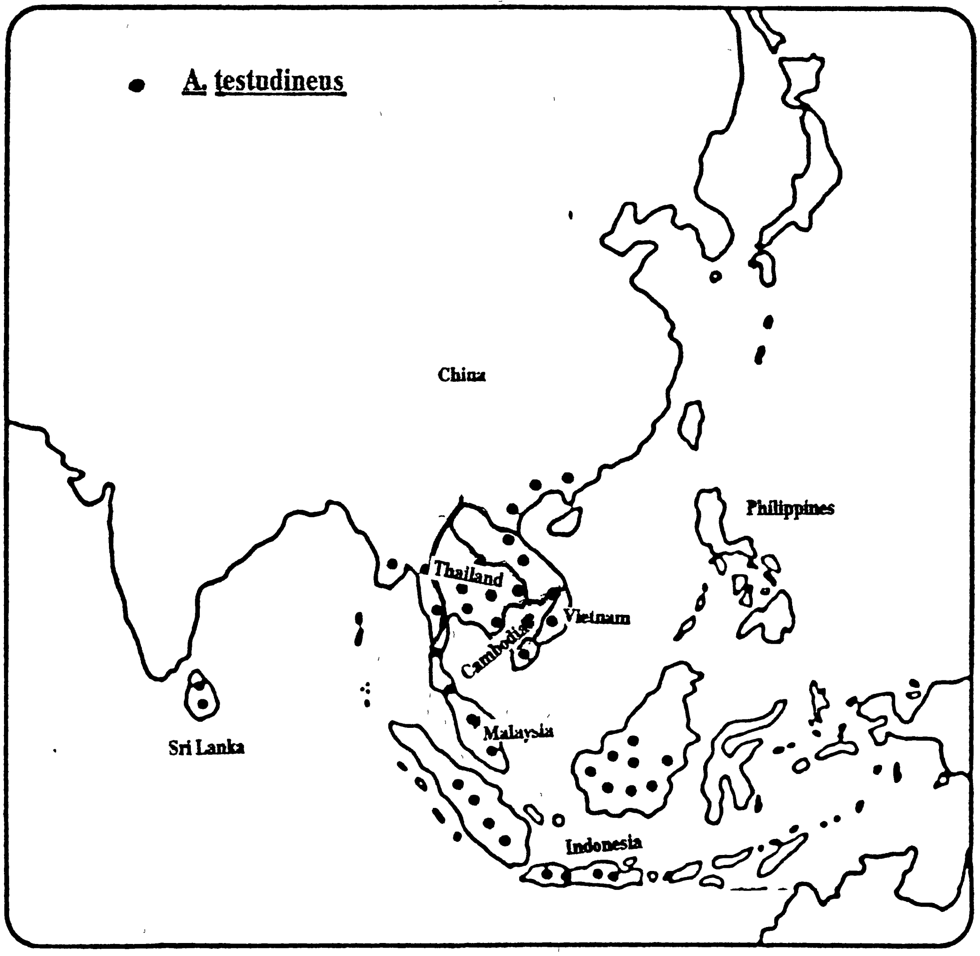


**Figure 3.** *General distribution of A. testudineus*

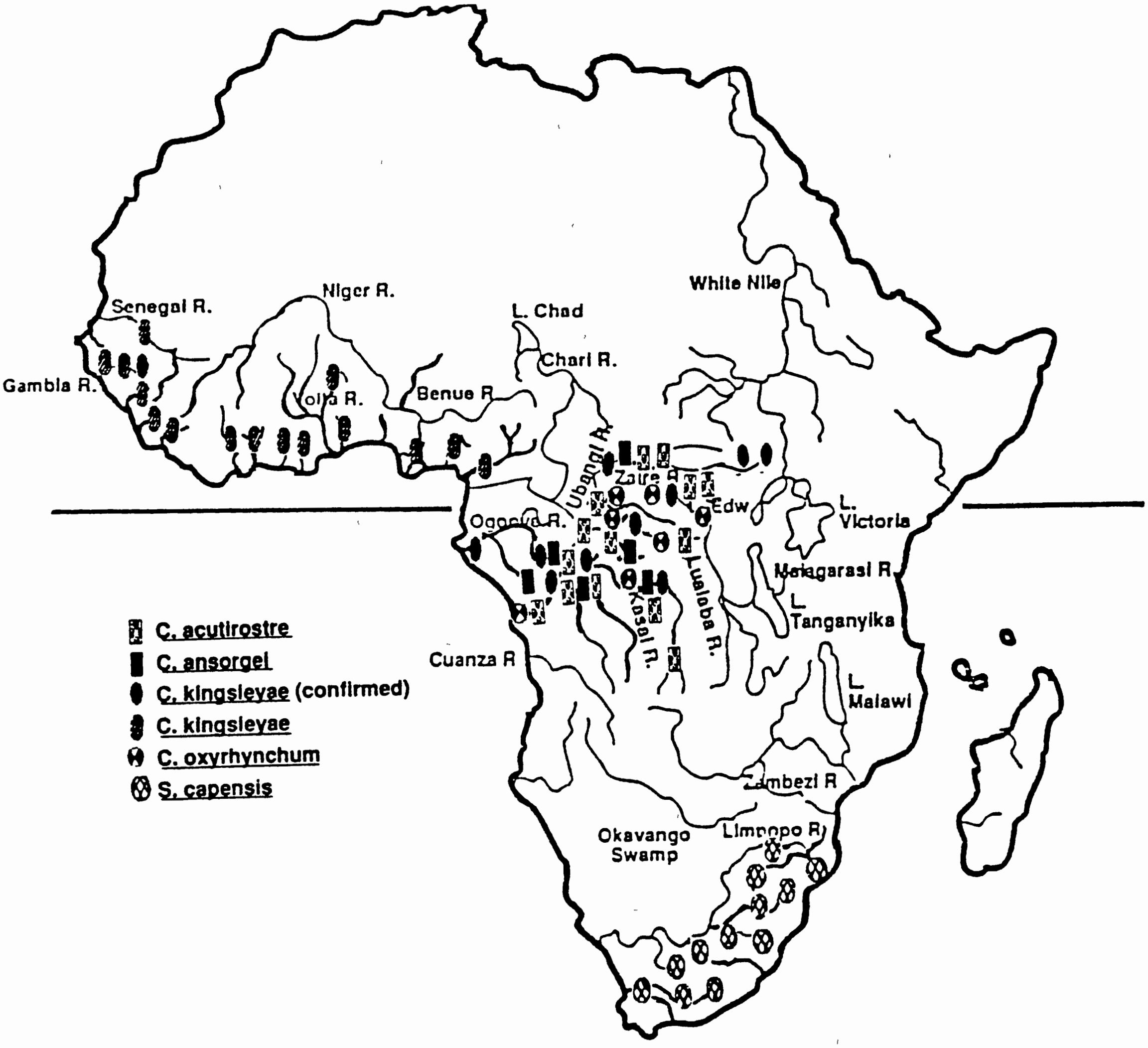


*Figure 4.* General distribution of *Ctenopoma* and *Sandelia* from Norris (1987)

Kasai River.

C. oxyrhynchum--almost exclusively found in the cuvette centrale in the lower reaches of the Sangha River and in the middle Kasai River.

C. ansorgei--lower and middle reaches of the cuvette centrale and to the Chiloango River.

## General Life History

A complete life history is not known for any of these species. Most Ctenopoma feed on arthropods although two species (C. acutirostre and C. ocellatum) show morphological adaptations for piscivory and are reported to feed on small fish in the wild (Norris 1987).

C. ansorgei (along with all species in the subgroup Nana) are bubblenest builders with the male providing care for eggs and fry. Other Ctenopoma in this study are free spawning, releasing natant eggs and displaying no parental care. Jubb (1967) reported that S. capensis build no nest but release eggs which sink and stick to substrate with the male providing care, however there are some indications they are bubblenest builders (Norris, 1987). A. testudineus lay natant eggs and provide no parental care (Goldstein, 1971). In the laboratory all Ctenopoma and Anabas appear to combine a loose hierarchy and territoriality into a flexible social system (personal observation). Miller and Miller (1970) noted a similar system in the Asian Anabantoids.

## Specimens Used

Wild-caught specimens of the six Anabantoid species were used for this study. The distribution of these fishes and their lack of popularity in the aquarium trade resulted in difficulty obtaining specimens. A waiting period of a year or more elapsed between ordering and receiving several species. Although attempts were made to obtain fishes from all three subgroups of Ctenopoma, most species that were requested could not be collected. All fishes were imported through New York and San Diego. All species were collected by professional collectors except for S. capensis, which was collected by Steven Norris with the cooperation of South African Fisheries and Museum personnel.

All fish shipments contained small numbers of young fish. Ctenopoma and Anabas were placed in 30-gal. population tanks, which contained plants and clay pots to provide cover. Several population tanks were maintained for each species as protection against disease and to provide conspecifics with different social experience for agonistic bouts. Because S. capensis are highly aggressive, they were isolated in 10-gal. aquaria to prevent injury. A total of 70 specimens were utilized in this study.

## Handling Techniques

Upon arrival, Ctenopoma and Anabas specimens were divided into several population groups, each of which was isolated and maintained in a population tank measuring 40.64 x 45.72 x 124.46 cm. These tanks contained assorted plastic plants, live Valisneria sp., small clay pots, and stacked rocks to provide hiding areas. All S. capensis were housed individually in tanks measuring 28 x 25 x 16.5 cm. Fluorescent lighting in the laboratory was set for a 12 hour photoperiod and no effort was made to block natural light from the windows. All the fish were fed flake food, live meal worms, and several types of commercially frozen foods: krill (Euphausia superba), brine shrimp (Artemia sp.), and blood worms. Approximately two inches of gravel covered the bottom of each tank. The tops of all aquaria were covered with glass or clear plastic. Water in the tanks was filtered through exterior charcoal filters, and standard aquarium heaters maintained water temperatures within a range of 24.3 and 27.9° C.

Agonistic bouts were staged in 20-gal. aquaria (40.5 x 26 x 28.5 cm.) excepting C. ansorgei and A. testudineus bouts. No plant cover or hiding places were provided during bouts. For visual convenience of the observer, the bout tanks were divided into three equal vertical sections by black tape placed on the outside of the glass. Staging agonistic bouts was difficult with C. ansorgei and A.

*testudineus*. These species would not fight in the large bout tank which had been used for the other *Ctenopoma* spp. and *S. capensis*. *C. ansorgei* would stay on their respective ends of the larger tank when the partition was removed. In a smaller fighting compartment 24 x 20 x 24 cm., the fish would not fight; they continuously swam up and down along the sides. I painted three sides of the small compartment opaque white, and isolated 12 of the *C. ansorgei* for three days in quart jars which had been painted black. These fish were isolated a minimum of three days. If at the beginning of a bout both fish were simultaneously placed into the small tank, fighting usually occurred within minutes. A. *testudineus* bouts were also staged in the small opaque compartment but the fish were moved directly from different population tanks to the bout tank, without isolation.

## Bout Protocols

Six diadic agonistic bouts were observed and videotaped for each species. Agonistic bouts were staged by placing two similarly sized conspecifics, from different population tanks, in either end of an observation tank. An opaque partition in the tank kept the fishes separate for at least 24 hours, allowing acclimatization. Upon removal of the partition the fish were video taped. Taping began with the initial contact between the fish and continued for 30 minutes, at which time it was terminated, regardless of the stage of the conflict.

I filmed with a Panasonic 3245 video camera (6X zoom lens) connected to a TV monitor. An internal timer recorded and displayed the time (minute and seconds) at the bottom of the screen. C. ansorgei and A. testudineus were filmed from behind a partition, which hid the camera and other filming activity; no partition was used while filming the other species. The room was darkened and incandescent lighting above the tank was used during taping. Whenever possible, both fish were continuously filmed. After the bout, both fish were placed in a third population tank. Because of the small number of fish and difficulties in stimulating agonistic behavior, some individuals were filmed more than once. However, no two fish were ever rematched. S. capensis individuals were returned to their isolation tanks and were matched only with new opponents. When filming was completed for a species, fish were maintained in large community tanks.

The tapes were viewed using a Mitsubishi HS-339U8 video cassette player/recorder, which allowed viewing of the tapes at several forward speeds and backwards. I used the tapes to establish an ethogram of agonistic behavior for each species. I coded the behaviors and recorded each behavior, qualifier, and time of each event in a notebook. This information was then entered into a computer using Lotus 123 or Quattro Pro (files are interchangeable within these two programs). Data for C. ansorgei and A. testudineus were typed directly into the computer without keeping a notebook. Data from all bouts were converted to ASCII files.

Each unit of behavior (behavioral act or display) provided four types of information: (1) major behavior (2) orientation to opponent (3) fin position and display posture and (4) repetitions of a movement. Numbers two and three are referred to in the discussion below as "qualifiers". After the behaviors for each fish in six bouts per species were noted, the data were analyzed using the SAS statistical package. The analysis was performed at several levels: (1) total number of behaviors per fish (2) total number of behaviors per bout (two fish) and (3) total number of behaviors per species (12 fish). An ANOVA was run to compare relative frequency of occurrence of each behavior among species with a F-test on the mean squares to compare significant variance at PR > F at .05. Additionally, an ANOVA MS between bouts per species was used as an error term to determine the effect of high levels of intraspecific variance. The Duncan's Multiple Range test was then used to determine specific species differences. A Chi-square statistic was calculated on the orientations to test for randomness.

A second data set was recorded on the middle ten minutes of each bout. The tape was stopped at two-second intervals and the fish were scored for their relative proximity to the opponent and position in the water column. These data were typed directly into the computer into Quattro Pro and converted to ACSII files for analysis. Means and standard deviations were calculated for these data.

Behaviors unique to a species are a significant finding. Such behaviors (apomorphies) were noted and weighted appropriately in the comparisons among species. Behavioral similarities among species were then compared to the recent phylogeny based on morphology (Fig. 2) presented by Norris (1987).

# CHAPTER III

# DESCRIPTION OF MAJOR BEHAVIORS AND QUALIFYING ORIENTATIONS

## Motor Patterns

The behaviors I used to study the Anabantoids are all easily recognized units that occurred frequently in the behavioral repertoire of several species or were unique to one species. I categorized 23 distinct behaviors (motor patterns) occurring in agonistic encounters; variations in orientation or intensity qualified (characterized) several of the behaviors. A complex unit of behavior is frequently a combination of simpler movements (Table II). A description of agonistic movements and qualifiers is presented here.

## Major Behaviors

AVOID -(AV)- An Avoid movement was an incomplete approach sequence. C. kingsleyae used this maneuver most often.

BODY QUIVER -(BQ)- The quivering fish displayed rapid, low amplitude lateral movements along the head and body. Miller and Miller (1970) note this behavior among common gourami species and equate it with vibrating. This movement did not result in a change of swimming direction. The

## TABLE II

## QUALIFIERS WHICH CHARACTERIZE OR MODIFY MAJOR BEHAVIORS

| Major Behavior | Orientation to Opponent | Fin Display | Head Display | Body Posture |
|---|---|---|---|---|
| Frontal approach | Anterior<br>Lateral<br>Posterior | Dorsal fin spread (full, 1/2, closed)<br>Pelvic fin spread (full, 1/2, closed)<br>Scull | Gular flair<br>Opercle spread | |
| Bite/Butt | Head<br>Body<br>Caudal | | | |
| Circle | Spin | | | |
| Fin Tug | Anal fin<br>Caudal fin<br>Dorsal fin<br>Pectoral fin<br>Pelvic fin | | | |
| Frontal display<br>Lateral display<br>Lateral presentation | Anterior<br>Lateral<br>Posterior | Dorsal fin spread (full, 1/2, closed)<br>Pelvic fin spread (full, 1/2, closed)<br>Arrow<br>Spike | Gular flair<br>Opercle spread | C-curve<br>Head down<br>Head up<br>Lean<br>Sigmoid curve<br>Shimmer |
| Tail Beat | Caudal/Caudal<br>Caudal/Head<br>Body/Head<br>Head/Caudal<br>Head/Head<br>Head/body | | | |

gourami species and equate it with vibrating. This movement did not result in a change of swimming direction. The Ctenopoma spp., excepting C. oxyrhynchum, frequently showed a Body Quiver. The other genera did not use the display often.

BUTTING-BITING -(B/B)- Butting involved pushing the mouth against the opponents body; Biting describes an attempt to grasp the opponent with the teeth (Miller and Miller 1968). I scored all movements of this type as a Butt-Bite. The area of the body attacked was a qualifying characteristic of this movement. C. oxyrhynchum frequently used the Bite/Butt and C. ansorgei used it the least.

CAROUSEL -(CAR)- Tooker and Miller (1980) describe carouseling fish as aligned in parallel, head to tail, both Laterally Displaying and simultaneously rapidly swimming in circles. C. ansorgei was the only species to Carousel.

CHASE -(CHA)- Whenever one fish actively pursued another fish which was trying to escape, a chase was scored. S. capensis used Chase most often, and A. testudineus was also a frequent user. The four Ctenopoma spp. chased infrequently.

CIRCLE -(Cir)- When circling, the fish swam away from its opponent then circled back to approach it. This behavior was distinguished from the Carousel by the lack of repeated rapid revolutions, and served to correct orientation for an approach sequence or display. The size of the arc and number of times a fish circled before orienting varied. *C. kingsleyae*, *C. ansorgei*, and A. *testudineus* Circled frequently.

DIGGING -(DIG)- A digging fish swam head down, perpendicular to the bottom of the tank, swimming up and down with the pectoral fins, pushing its mouth into the gravel. Often the fish would spit gravel from its mouth after a digging sequence. *A. testudineus* was the only species exhibiting Digging.

FLEE -(FLEE)- A Fleeing fish actively tried to avoid contact with a pursuing fish. *A. testudineus* was the species which would Flee most often.

FIN TUGGING -(FT)- As described by Miller & Miller (1970), a fish grasps the fin of another and jerks violently, often displacing the other fish. Idenitity of the tugged fin served as a qualifier for this behavior. The highly aggressive *S. capensis* was the most frequent Fin Tugging species.

FOLLOW -(FOL)- A Follow was scored whenever one fish slowly followed another fish that was not trying to escape. *A. testudineus* used this behavior most; however, it was not a frequent behavior for any of the species studied.

FRONTAL APPROACH -(FAPP)- A movement which involved any direct, forward movement of one fish toward another. The approaching fish faced the opponent. Frontal Approach was a complex behavior pattern, which could include variable median fin extension, Opercle Spread, and Gular Flair (see below). The degree of fin spread and the presence of Opercle Spread or Gular Flair seemed dependent upon motivational intensity and orientation. Other qualifiers include Scull and Arrow, which are described in the next section. Frontal Approaches were frequently followed by either an Avoid movement, Tail Beating or Mouth Fighting. C. kingsleyae and A. testudineus Frontally Approached frequently.

FRONTAL DISPLAY -(FD)- A complex motor pattern, involved the Gular Flair, Opercle Spread, raised median fins, and Head Jerks. One fish approached another using this display. Frontal Display presented the opponent with a view of maximum head area. A Frontal Approach involved many of the same motor patterns; therefore, a Frontal Display was scored only if the displaying fish ceased to approach the opponent and maintained the displaying posture. C. ansorgei used Frontal Display most often.

HEAD JERK -(HJ)- A Head Jerk involved a quick lateral snapping of the head in either direction. A change in swimming direction or orientation followed the Head Jerk. Several jerks often occurred in quick succession, and were frequently seen in complex behavior patterns. This behavior was seen most often during A. testudineus bouts.

LATERAL DISPLAY -(LD)- The displaying fish used a lateral orientation anterior or parallel to the opponent.

The median fins, caudal fin, and opercles are spread to varying degrees. This complex motor pattern may include a Sigmoid Curve, or C-Curve. Lean or tilt of the body and orientation of the head may also vary. Intensity (amount of fin erection) and orientation qualified this behavior. This suite of movements was scored a Lateral Display if it occurred more than one body length from the opponent. *C. acutirostre* utilized the Lateral Display most often, almost 40% of their total acts were Lateral displays.

LATERAL PRESENTATION -(LP)- Lateral Presentation involved the same movements as the Lateral Display but it occurred less than one body length from the opponent. LP was used in intense fighting, and combined a signal (threat) and displacement move. Thirty percent of the total behaviors for *S. capensis* were Lateral Presentations.

MOUTH FIGHTING -(MF)- During a Mouth Fight the fish grasped each other by the mouth, pushing and pulling one another around the tank. These episodes lasted several seconds and occurred during intense fighting. A modified form of Mouth Fighting was seen in *C. kingsleyae*. The fish oriented head to head in full Frontal Display and snapped their mouths open and closed. Each fish moved back with the force of the snap, swam forward and snapped again. No contact was made during this behavior (Fig. 5). Only two species used the Mouth Fight, *C. kingsleyae* and C. *oxyrhynchum*.

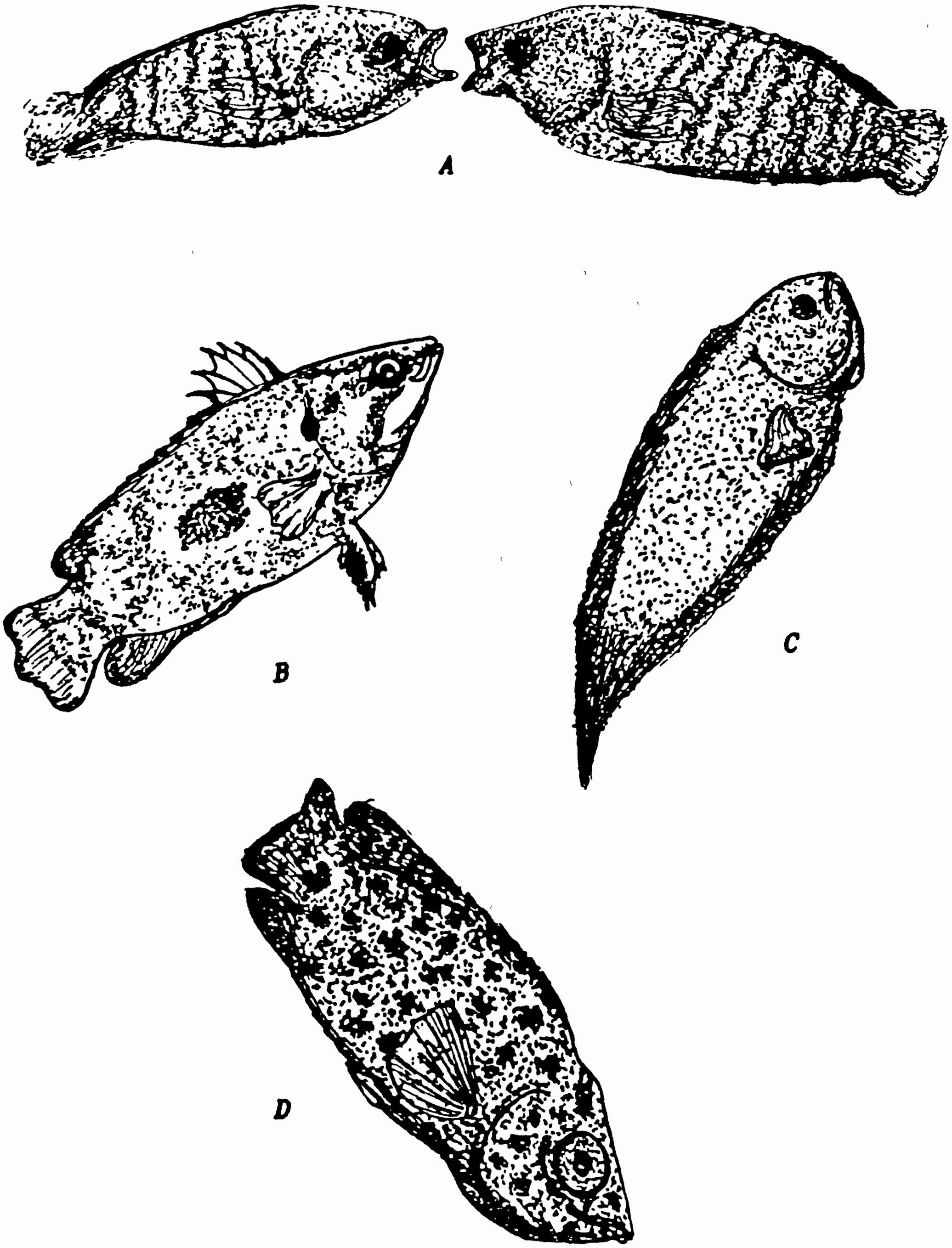


Figure 5. Complex display patterns associated with species use: (A) Mouth snap fight, (B) Spike, (C) Arrow, (D) Charging

SWIM BACKWARD INTO OTHER FISH -(SBTOF)- A fish positions itself anterior to its opponent and swim backwards, using only the pectoral fins. This resulted in the displacement of the opponent. Three cryptically marked species (*C. acutirostre*, *C. oxyrhynchum*, and *C. ansorgei*) were the most frequent users of the SBTOF.

REST - A rest was scored only when a fish sat on the gravel with all its fins closed.

SWIM OVER BODY -(SOB)- One fish swims over the other fish, pushing the opponent down by dragging its ventral surface across the opponent's dorsal area. This behavior was rare in all bouts but used most frequently by *S. capensis*.

SWIM UNDER BODY -(SUB)- The actor swims under the opponent and displaces it by pushing up with the dorsal area of the head or body. The acting fish may the opponent and continue to push up for several seconds. This displacement pattern was seen most often in *C. oxyrhynchum* bouts.

SWIM SIDEWAYS INTO OTHER FISH -(SSTOF)- This movement was used when the fish were parallel and one fish used the pectoral fins to swim laterally into its opponent. This movement often resulted in the displacement of the opponent. Used most often by *S. capensis*, this behavior comprised ten percent of the total behaviors for this species.

TAIL BEAT -(TB)- Miller (1964) described a Tail Beat as occurring during lateral display and consisting of slow, powerful thrusts of the tail and caudal peduncle toward the other fish while the pectoral fins prevented forward swimming. This behavior occurred while the fish were positioned at various parallel orientations and some species preference for orientation was shown. Tail Beating could be reciprocal or nonreciprocal. The number of thrusts in a sequence seemed to indicate intensity. The Tail Beat is used most often by *S. capensis*.

TAIL SWEEP -(TS)- The Tail Sweep involved dragging the caudal fin along the body of an opponent. This was done without force and the opponent was not displaced. Generally, the Tail Sweep was incorporated into a circling move as the Sweeping fish swam away. Often it was seen late in a bout when the dominant fish swam close to its opponent to facilitate Tail Sweep.

### Qualifiers Which Characterize or Modify Major Behaviors

ARROW -(AOW)- This posture was seen during Lateral Displays, Lateral Presentations, Frontal Displays, and Frontal Approaches. A Gular Flair and Opercle Spread were simultaneously presented while caudal and median fins were closed, giving the body a streamlined appearance and the head a large triangular shape (Fig. 5). Arrow was only observed in *C. ansorgei*. During the display the body of this normally brightly colored fish paled completely, leaving black at the edges of the folded fins.

C-CURVE -(C-cv)- As a qualifier for Lateral Display and Frontal Display the C-Curve was a lateral curving of the body into a "C" shape, head and tail pointing in the same direction. The curving fish could use its pectoral fins to swim toward or away from the opponent. C-curve was used predominantly by *C. acutirostre* and *C. ansorgei*, two species which hide in plant cover.

GULAR FLAIR -(GF)- The gular area, below the operculum, is spread and flared resulting in an enlarged visual appearance laterally and frontally. Gular Flair was integral to any display which relied on increased apparent body size. The degree of flair seemed relative to the intensity of the bout. Presentation of the Gular Flair generally coincided with use of the Opercle Spread (Figs. 6, 7).

LEAN -(LEAN)- A displaying fish would tilt the median axis, dorsal spines raised, toward or away from its opponent. This was a qualifying movement seen as part of many complex behaviors. The Lean was seen in appeasement behaviors and also used aggressively to displace opponents. This behavior is used most by *C. oxyrhynchum* and *S. capensis*, the most aggressive species studied.

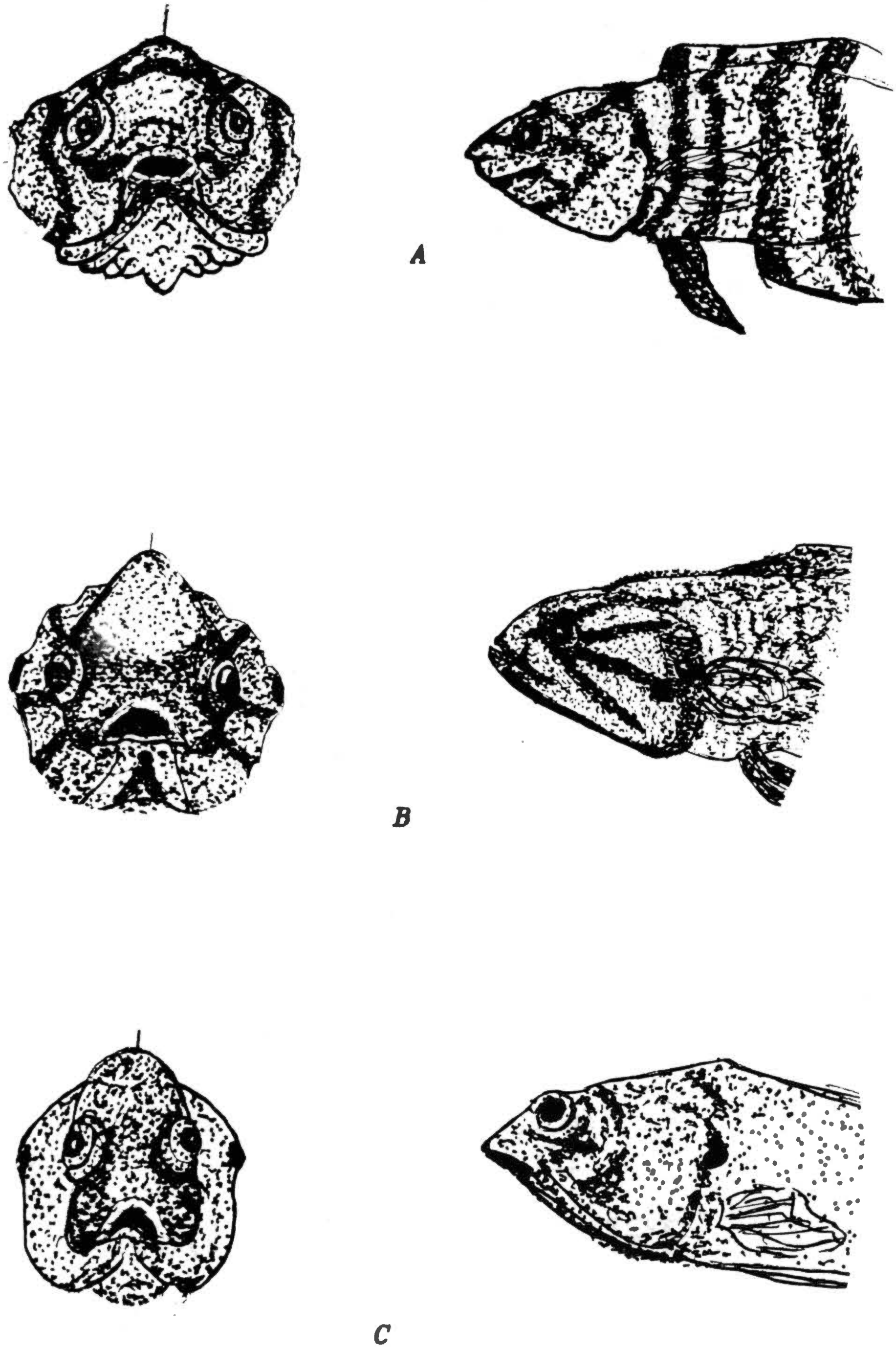


Figure 6. Frontal and lateral view of Opercle Spread and Gular Flair: (A) *C. ansorgei*, (B) *S. capensis*, (C) *A. testudineus*

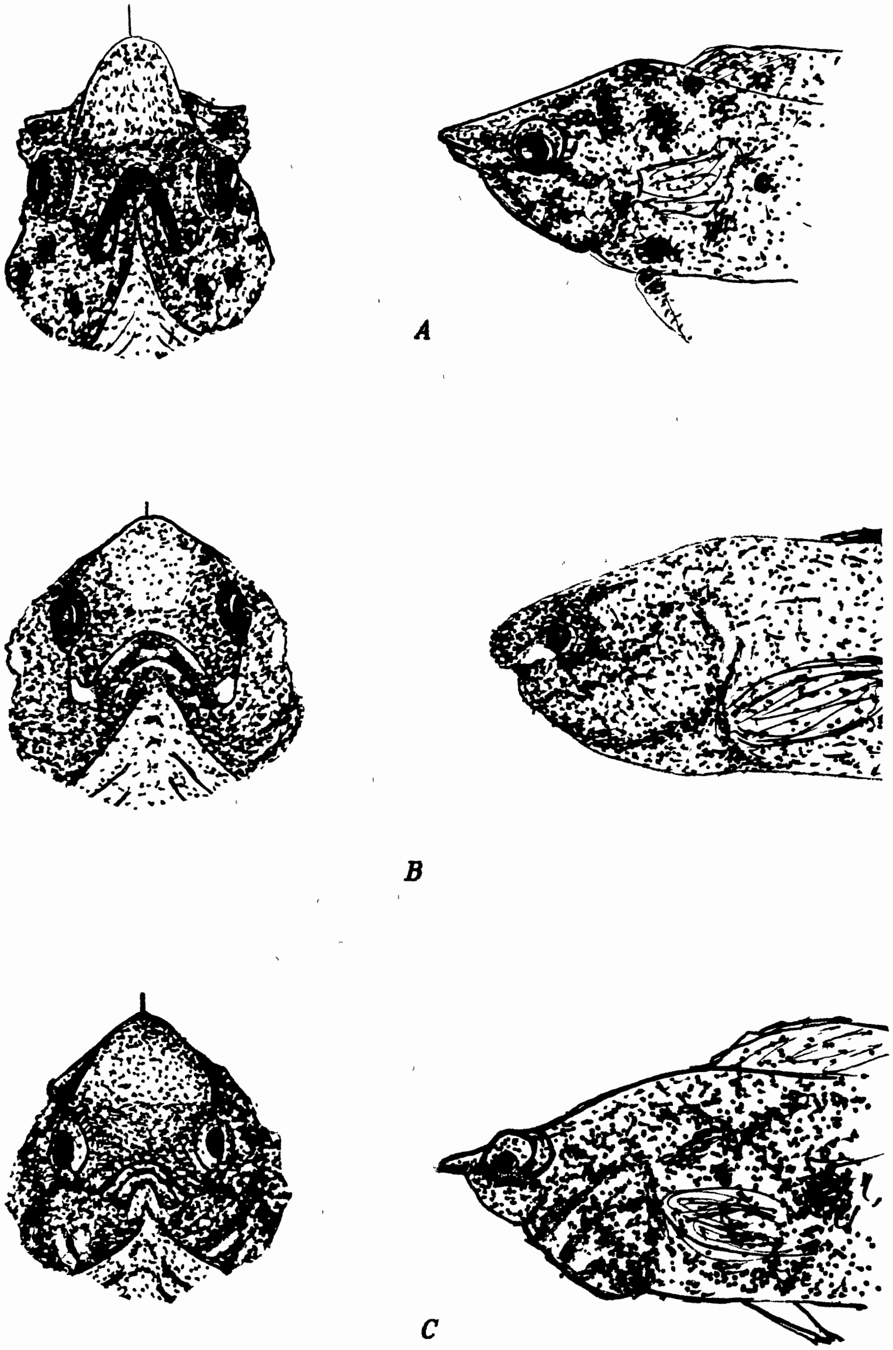


Figure 7. Frontal and lateral view of Opercle Spread and Gular Flair: (A) *C. acutirostre*, (B) *C. kingsleyae*, (C) *C. oxyrhynchum*

OPERCLE SPREAD -(OP)- Described by Miller and Miller (1970) as Gill-cover erection which involves moving the opercle forward to visually present an enlarged frontal projection. Opercle Spread was seen in many complex motor patterns; degree of spreading appeared to vary with species and bout intensity (Figs. 6, 7).

CHARGING -(CHARGE)- While charging, a Frontal Approaching fish would lower its head, present a Gular Flair, Opercle Spread, closed median fins, and swim in a direct line toward the opponent using only its pectoral fins. From a lateral view, the fish appeared to bend the body, lowering the head, just behind the opercles in the predorsal area. The open caudal fin and direct approach distinguished this behavior from the Arrow (Fig. 5). This approach appeared threatening but often was followed by an Avoid movement.

SHIMMER -(SHIM)- This behavior involved exaggerated caudally progressing undulations of the body. The Shimmering fish often rotated the median axis of the body to increase the lateral area displayed to an opponent. The Shimmering undulations could be displayed while swimming or while stationary. The behavior often appeared while swimming "in place" or was performed while swimming, but the undulations did not appear to increase the swimming speed. The Shimmering fish would often swim in front of an opponent, slow down, tilt the body, and insert several extra undulations into the swimming pattern before circling away. This behavior was unique to *A. testudineus*.

SIGMOID CURVE -(SIG)- A lateral curving of the body axis into an "S" posture. The head was pointed up or down during this curve. *C. acutirostre* and C. *ansorgei* used this body position most often.

SPIKE -(SPK)- Spike was a qualifier of the Lateral Display and Lateral Presentation. The first few rays of the dorsal fin were raised with the remainder of the fin closed. The number of rays raised and the angle of fin erection reflected intensity of this movement but were not scored (Fig. 5). This behavior was often present while the fish rested on the gravel.

SPIN -(SP)- A circle rapidly executed with a small arc was qualified as a spin. The Spin often occurred during intense fighting. *S. capensis* used the Spin most frequently.

TAIL BEAT ORIENTATION -(TBO)- Tail Beating was qualified by six orientations (Fig. 8). Some of the orientations were species specific; in other instances a species used several orientations but showed a larger frequency of one orientation.

Head/Caudal -(H/C)- The fish aligned parallel and lateral to each other. They were positioned head to caudal and less than one body length apart. As one fish beats its tail against the opponent, a reciprocal slap was performed

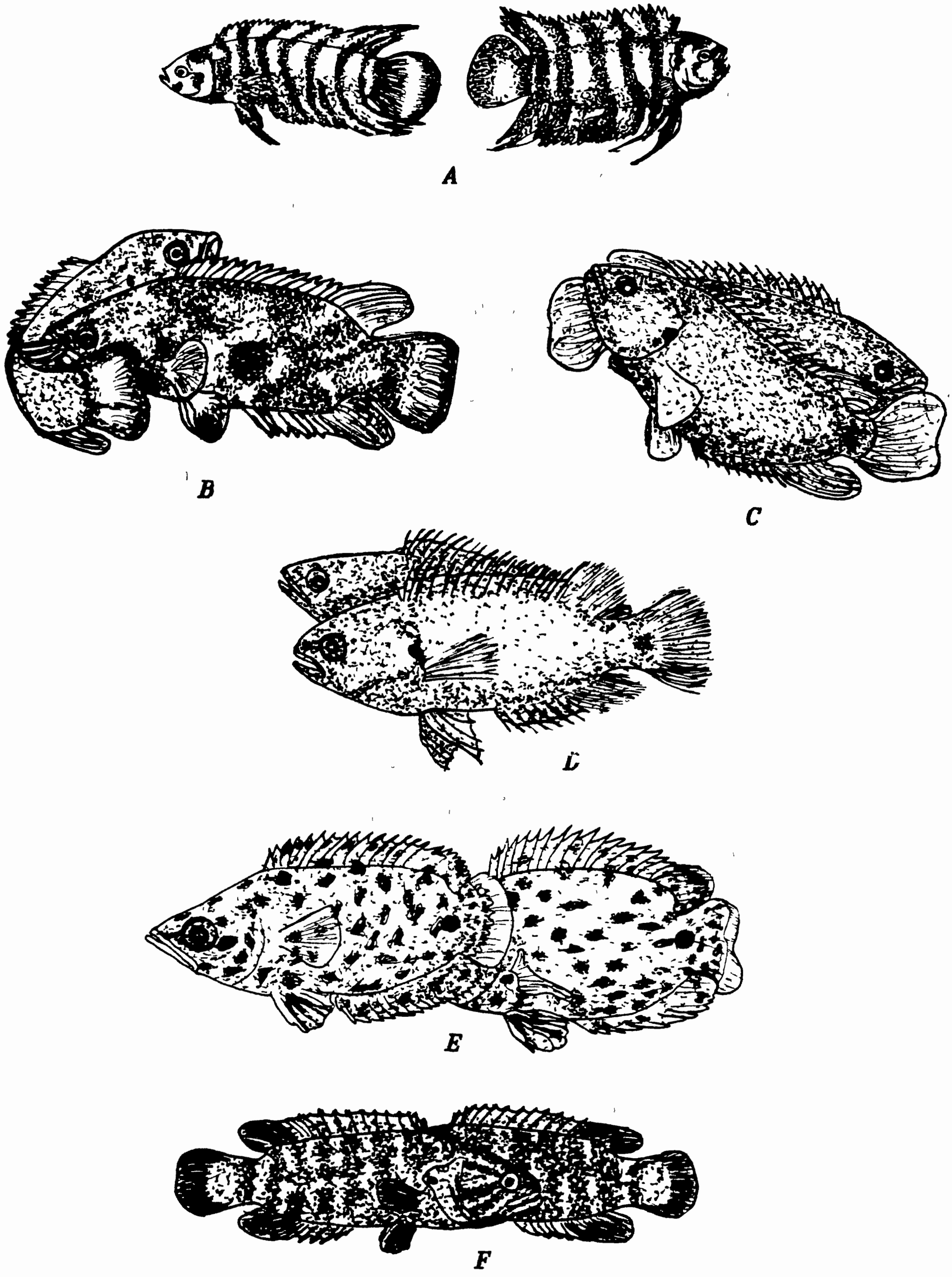


Figure 8. Tail Beating orientations. (A) Caudal/Caudal, (B) Body/Head, (C) Head/Caudal, (D) Head/Head, (E) Caudal/Head, (F) Head/Body

by the other fish. The pair often beat, circled in unison, and beat again. This sequence could be repeated several times. This is the only form of Tail Beating which by definition must be reciprocal.

Full Body/Head -(B/H)- The Tail Beating fish curved its body around the head of the opponent and alternately slammed into the other fish with its head and tail. The pectoral fins were used to maneuver closer to the opponent. This form of Tail Beating often followed a Bite/Butt to the body by the opponent.

Head/Body -(H/B)- The fish aligned parallel and laterally, within one body length. The head and opercle area of each fish was at the mid-body area of the opponent. The fish swam anteriorly or posteriorly to maintain this orientation. Large, powerful undulations were made with the tail which caused the head of the beating fish to slam into the body of its opponent. These blows were often sufficiently powerful to displace the opponent. The fish did not beat simultaneously, but often alternated Tail Beats.

Head/Head -(H/H)- The fish aligned parallel and laterally, head to head. The beating fish slapped the opponents head with its tail. This form of Tail Beating was used while both fish were swimming.

Caudal/Caudal -(C/C)- The fish were facing opposite directions, and could swim backwards to align with an opponent. The beating fish would make large, powerful caudal undulations. Frequently the tails of the fish were not in contact, however, the force of the undulation resulted in slightly displacing the opponent. Caudal/Caudal Tail Beating was commonly used in a reciprocal sequence.

Caudal/Head -(C/H)- This form of Tail Beating could occur whenever one fish was directly anterior another. This occurred if one fish approached another posteriorly or if one fish swam in front of the other and stopped. The Tail Beating fish frequently stopped swimming to facilitate proximity for the Tail Beat. This form of Tail Beating is repeatedly seen in response to a caudal Bite/Butt.

# CHAPTER IV

# RESULTS

## Frequency of Individual Acts

There were 23 distinct major motor patterns that were utilized in agonistic encounters by the species studied. When orientation patterns were documented as significant qualifying attributes, an additional 31 categories were recognized (Table II) bringing the total number of unique behavioral "units" to 54. A combination of seven major motor patterns and qualifiers were unique to a species by presence or absence and documented as apomorphic behaviors (Table III). The first analytical step undertaken was an ANOVA test conducted on the frequencies of the 21 major patterns (Table IV).

The ANOVA two way analysis of variance (percent behaviors by species) revealed the behaviors had significantly different relative frequencies. The ANOVA MS between bouts per species was used as the error term for intraspecific variance and the F-ratio was calculated on the means of each behavior to test for homogeneity of variance (Table IV). The behaviors were significant at less than the

## TABLE III

## SPECIES APOMORPHIC BEHAVIORS AND QUALIFIERS

| Motor Pattern | Species | Presentation |
|---|---|---|
| Digging | *A. testudineus* | + |
| Fin Tug | *A. testudineus* | - |
| Shimmer | *A. testudineus* | + |
| Carousel | *C. ansorgei* | + |
| Arrow | *C. ansorgei* | + |
| Tail Beat (Head/Body) | *S. capensis* | + |
| Mouth Fight (Snap) | *C. kingsleyae* | + |

(+)motor pattern used; (-)moter pattern not used

## TABLE IV

## ANALYSIS OF VARIANCE ON PERCENT BEHAVIOR BY SPECIES

| Behavior | Mean Square Error | F-Value | PR > F |
|---|---|---|---|
| Avoid | 0.0035 | 17.55 | 0.0001 |
| Bite/Butt | 0.0192 | 9.81 | 0.0001 |
| Body Quiver | 0.0091 | 9.3 | 0.0001 |
| Chase | 0.0003 | 2.84 | 0.022 |
| Circle | 0.0339 | 34.54 | 0.0001 |
| Frontal Approach | 0.1104 | 15.26 | 0.0001 |
| Follow | 0.0011 | 10.18 | 0.0001 |
| Fin Tug | 0.0002 | 17.9 | 0.0001 |
| Head Jerk | 0.0216 | 25.68 | 0.0001 |
| Lateral Display | 0.1363 | 26.65 | 0.0001 |
| Lateral Presentation | 0.1129 | 26.85 | 0.0001 |
| Mouth Fight | 0.0001 | 6.22 | 0.0001 |
| Rest | 5E-05 | 3.3 | 0.0101 |
| SBTOF | 0.0042 | 15.79 | 0.0001 |
| SOB | 0.0001 | 2.54 | 0.0364 |
| SUB | 0.0003 | 7.11 | 0.0001 |
| SSTOF | 0.0161 | 43.26 | 0.0001 |
| Tail Beat | 0.0683 | 63.86 | 0.0001 |
| Tail Sweep | 0.0006 | 6.88 | 0.0001 |

Model df = 5, Error df = 66

0.05 alpha level, indicating a rejection of the null hypothesis (that observed differences between the mean squares of the species was due to random variability, Schmidt, 1975; Martin and Bateson, 1988). The Duncan's Multiple Range test was used to determine specific species differences (Table V).

A summary of the Duncan's Multiple Range test (Table VI) revealed large numbers of significant differences between *A. testudineus* and all other species. *S. capensis* also had a large number of significant differences with all species (12 to 14). Of the four *Ctenopoma* spp., *C. oxyrhynchum* exhibited the greatest differentiation from all other species, differing in 10 to 20 behaviors from each other species. Interestingly, *C. ansorgei*, the sole member of the *Nana* subgroup, showed the least differentiation of all *Ctenopoma* spp. As will be discussed in the next section, *C. ansorgei* appears to utilize color pattern changes more prominently in social communication, and tends to have a more generalized motor pattern repertoire than its congeners. Though one might expect that the three deep-bodied members of the "Monkengia" species group would show the greatest similarities in patterns of act frequencies, Table VI reveals that they differ significantly from one another in 9 to 12 behaviors.

Overall patterns of act use were unique for each species studied. Though most of the major motor patterns

## TABLE V

## DUNCAN'S MULTIPLE RANGE GROUPING OF MAJOR BEHAVIORS

| BEHAVIOR | | | DUNCAN GROUPING | | Alpha = 0.05 | df = 66 |
|---|---|---|---|---|---|---|
| BODY QUIVER | *C. kingsleyae* | *C. acutirostre* | *C. ansorgei* | *C. oxyrhynchum* | *A. testudineus* | *S. capensis* |
| FRONTAL DISPLAY | *C. ansorgei* | *A. testudineus* | *S. capensis* | *C. kingsleyae* | *C. oxyrhynchum* | *C. acutirostre* |
| TAIL BEAT | *S. capensis* | *C. oxyrhynchum* | *C. ansorgei* | *C. acutirostre* | *C. kingsleyae* | *A. testudineus* |
| LATERAL DISPLAY | *C. acutirostre* | *C. ansorgei* | *C. kingsleyae* | *C. oxyrhynchum* | *A. testudineus* | *S. capensis* |
| LATERAL PRESENT. | *S. capensis* | *C. oxyrhynchum* | *C. acutirostre* | *A. testudineus* | *C. kingsleyae* | *C. ansorgei* |
| HEAD JERK | *A. testudineus* | *C. ansorgei* | *C. kingsleyae* | *C. acutirostre* | *C. oxyrhynchum* | *S. capensis* |
| MOUTH FIGHT | *C. kingsleyae* | *C. oxyrhynchum* | *S. capensis* | *C. ansorgei* | *C. acutirostre* | *A. testudineus* |
| TAIL SWEEP | *C. oxyrhynchum* | *S. capensis* | *C. acutirostre* | *C. kingsleyae* | *A. testudineus* | *C. ansorgei* |
| BITE/BUTT | *C. oxyrhynchum* | *C. kingsleyae* | *C. acutirostre* | *S. capensis* | *A. testudineus* | *C. ansorgei* |

TABLE V (Continued)

| BEHAVIOR | | | DUNCAN'S GROUPING | | ALPHA = 0.05 | df = 66 |
|---|---|---|---|---|---|---|
| SBTOF | *C. acutirostre* | *C. ansorgei* | *C. oxyrhynchum* | *S. capensis* | *C. kingsleyae* | *A. testudineus* |
| SSTOF | *S. capensis* | *C. oxyrhynchum* | *C. acutirostre* | *C. ansorgei* | *C. kingsleyae* | *A. testudineus* |
| CHASE | *A. testudineus* | *C. ansorgei* | *C. kingsleyae* | *C. acutirostre* | *C. oxyrhynchum* | *S. capensis* |
| AVOID | *C. kingsleyae* | *C. acutirostre* | *A. testudineus* | *C. oxyrhynchum* | *C. ansorgei* | *S. capensis* |
| CIRCLE | *A. testudineus* | *C. kingsleyae* | *C. ansorgei* | *C. oxyrhynchum* | *S. capensis* | *C. acutirostre* |
| FAPP | *C. kingsleyae* | *A. testudineus* | *C. acutirostre* | *C. ansorgei* | *C. oxyrhynchum* | *S. capensis* |
| SUB | *C. oxyrhynchum* | *C. kingsleyae* | *S. capensis* | *C. acutirostre* | *C. ansorgei* | *A. testudineus* |
| SOB | *S. capensis* | *C. oxyrhynchum* | *C. acutirostre* | *C. kingsleyae* | *C. ansorgei* | *A. testudineus* |
| REST | *S. capensis* | *A. testudineus* | *C. ansorgei* | *C. acutirostre* | *C. kingsleyae* | *C. oxyrhynchum* |

TABLE V (Continued)

| BEHAVIOR | | | DUNCAN'S GROUPING | | ALPHA = 0.05 | df = 66 |
|---|---|---|---|---|---|---|
| FOLLOW | *A. testudineus* | *C. kingsleyae* | *C. ansorgei* | *C. oxyrhynchum* | *C. acutirostre* | *S. capensis* |
| FLEE | *A. testudineus* | *C. ansorgei* | *C. kingsleyae* | *C. acutirostre* | *C. oxyrhynchum* | *S. capensis* |
| FIN TUG | *S. capensis* | *C. ansorgei* | *C. oxyrhynchum* | *C. acutirostre* | *C. kingsleyae* | *A. testudineus* |

## TABLE VI

## SUMMARY OF DUNCAN'S SPECIES GROUPING OF BEHAVIORS AND QUALIFIERS

| Species x | Species | Significant Differences | Apomorphies | Total |
|---|---|---|---|---|
| *A. testudineus* | *C. acutirostre* | 15 | 3 | 18 |
| | *C. kingsleyae* | 12 | 4 | 16 |
| | *C. oxyrhynchum* | 17 | 3 | 20 |
| | *C. ansorgei* | 10 | 5 | 15 |
| | *S. capensis* | 15 | 2 | 17 |
| *S. capensis* | *C. acutirostre* | 13 | 1 | 14 |
| | *C. kingsleyae* | 14 | 2 | 16 |
| | *C. oxyrhynchum* | 11 | 1 | 12 |
| | *C. ansorgei* | 11 | 3 | 14 |
| | *A. testudineus* | 15 | 4 | 19 |
| *C. ansorgei* | *C. acutirostre* | 6 | 2 | 8 |
| | *C. kingsleyae* | 6 | 3 | 9 |
| | *C. oxyrhynchum* | 11 | 2 | 13 |
| | *S. capensis* | 11 | 3 | 14 |
| | *A. testudineus* | 10 | 5 | 15 |
| *C. acutirostre* | *C. kingsleyae* | 8 | 1 | 9 |
| | *C. oxyrhynchum* | 10 | 0 | 10 |
| | *C. ansorgei* | 6 | 2 | 8 |
| | *S. capensis* | 13 | 1 | 14 |
| | *A. testudineus* | 15 | 3 | 18 |
| *C. kingsleyae* | *C. acutirostre* | 8 | 1 | 9 |
| | *C. oxyrhynchum* | 12 | 1 | 13 |
| | *C. ansorgei* | 6 | 3 | 9 |
| | *S. capensis* | 14 | 2 | 16 |
| | *A. testudineus* | 12 | 4 | 16 |
| *C. oxyrhynchum* | *C. acutirostre* | 10 | 0 | 10 |
| | *C. kingsleyae* | 12 | 1 | 13 |
| | *C. ansorgei* | 11 | 2 | 13 |
| | *S. capensis* | 11 | 1 | 12 |
| | *A. testudineus* | 17 | 3 | 20 |

Alpha = 0.05

were exhibited by all of the species, each species showed some unique patterns of greater or reduced frequency of act use. The ANOVA and Duncan's analysis show only one aspect of these variations among species, but they demonstrate that frequencies of acts do differ among species. Reasons for these differences can only be speculated on at this stage of the study, but they could be due as much, or more, to recent influences of ecological imperatives as to heritable factors associated with recent common ancestry. In the next section, a detailed account of fighting behavior will be presented for each species in order to present a more comprehensive picture of how fighting actually differs among the species studied. Where possible, frequency patterns of all 54 behavioral acts studied will be referred to in order to show unique patterns or identify symmetries or asymmetries among the species. Comments on ecological factors (derived from observations on fish in community tanks or from literature) that may have relevance in comprehending a particular species pattern will also be included in this section.

## Species Behaviors

Each species presented a generalized behavior pattern which was recognizable as Miller and Hall (1968) reported in their study of *Trichogaster* leeri. These generalized patterns may result from certain types of behavior becoming distinctively modified in each species during evolution to serve as threats, intimidate rivals, and reduce fighting (Manning, 1979). The evolved displays within this taxon may have been constrained or shaped by adaptations to tropical environments for the African species sympatric in the *cuvett centrale* and to a temperate environment for *S. capensis*.

## *C. acutirostre*

Commonly called the leopard fish, this species inhabits weedy waters, is cryptically marked, and is an ambush predator (Pinter, 1984). This trophic strategy requires restrained activity which was reflected in the species general activity pattern. *C. acutirostre* had the lowest relative frequency of major agonistic behaviors among the species studied (Fig. 9). Fish sat on the gravel bottom, leaning against the sides of the tank or hidden within plant cover. During feeding they darted out, fed, and darted back into hiding. As they matured the striking spotted color pattern became less distinct and they spent less time hiding. However, older fish still leaned against the side of the tank or other fish, and were often observed grouped together in a corner or in plant cover. Agonistic behavior, in population tanks, began only if one fish tried to displace another by leaning and pushing.

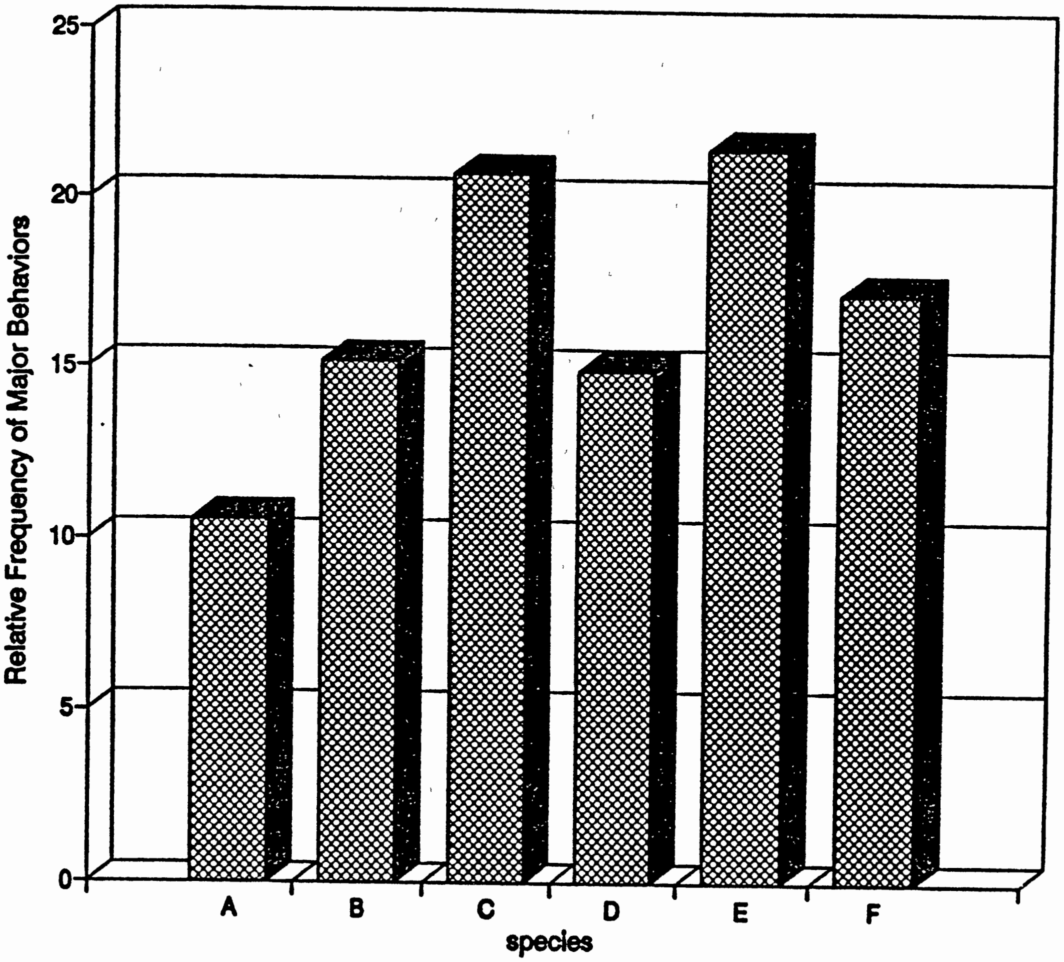


Figure 9. Relative Frequency for each species of all major behaviors. Species: (A) *C. acutirostre*, (B) *C. kingsleyae*, (C) *C. oxyrhynchum*, (D) *C. ansorgei*, (E) *S. capensis*, (F) *A. testudineus*

Prior to beginning the timed bouts, but after the partition was removed, these fish often remained at opposite ends of the tank resting on the gravel for 15 minutes or longer, before making initial contact. If any disturbance occurred in the filming area during this time, the fish would not approach one another. This species displayed two distinct fighting patterns; a slow moving, visually oriented pattern and an active, tactile oriented pattern. The fish were sensitive to any noise or movement around the tank during low intensity fighting, which consisted mostly of visual displays (LP and LD) and the low-disturbance supplanting behaviors SBTOF, SOB, and SSTOF (Fig. 10). Lateral Displays and Presentations often incorporated qualifiers that involved the full-body motor patterns of C-curving, Sigmoiding, and Body Quivers (Fig. 11). This species showed a bias for the Lateral Display, generally presenting all displays with a lateral orientation to the opponent (Figs. 12, 13, 14). However, displays were performed behind the opponent with higher relative frequency than in other species studied. This generally occurred whenever an approaching fish (SBTOF) began moving toward the other. During intense agonistic encounters, the fish were not easily distracted and they would Circle and Frontally Approach the opponent laterally (Fig 15) using Bite/Butt and Tail Beating sequences (Figure 16). The species displayed a bias for biting and butting the lateral area of the "body"

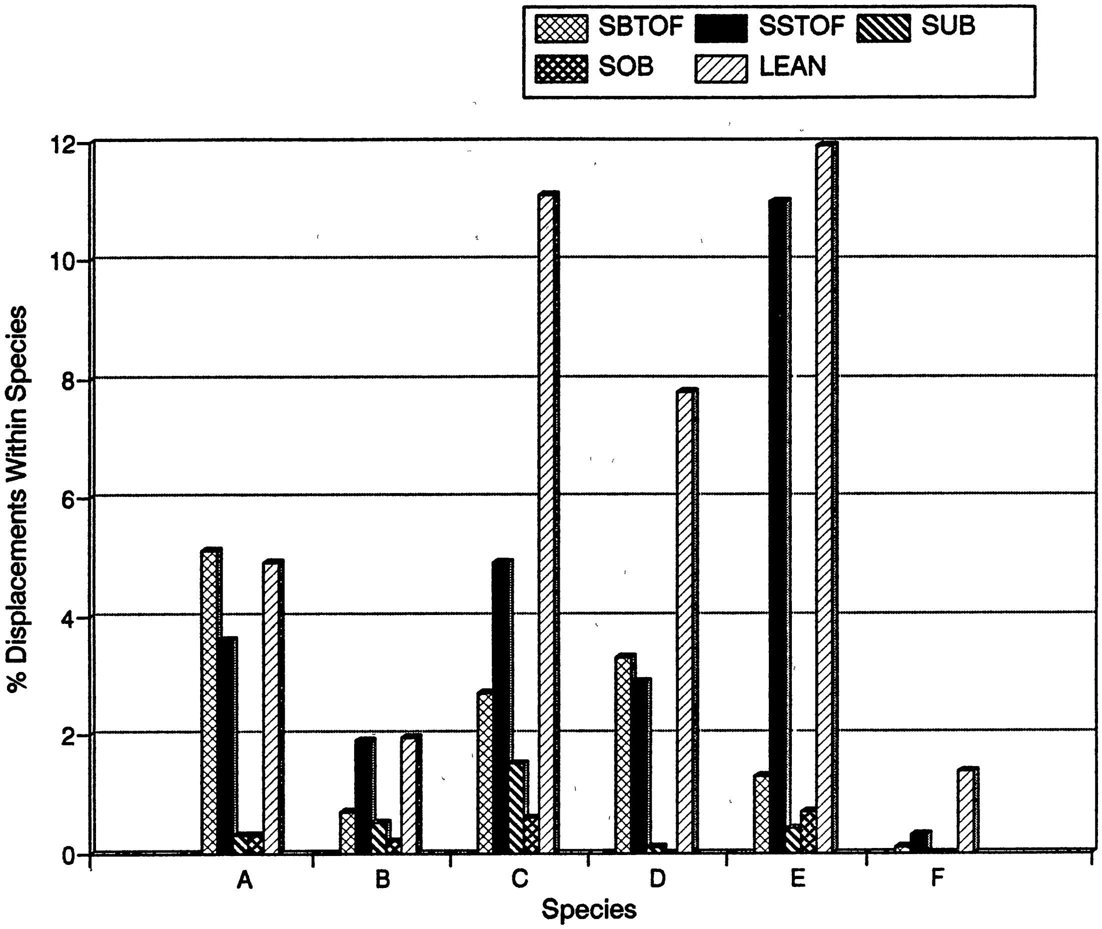


Figure 10. Relative frequency for each species of displacement moves. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

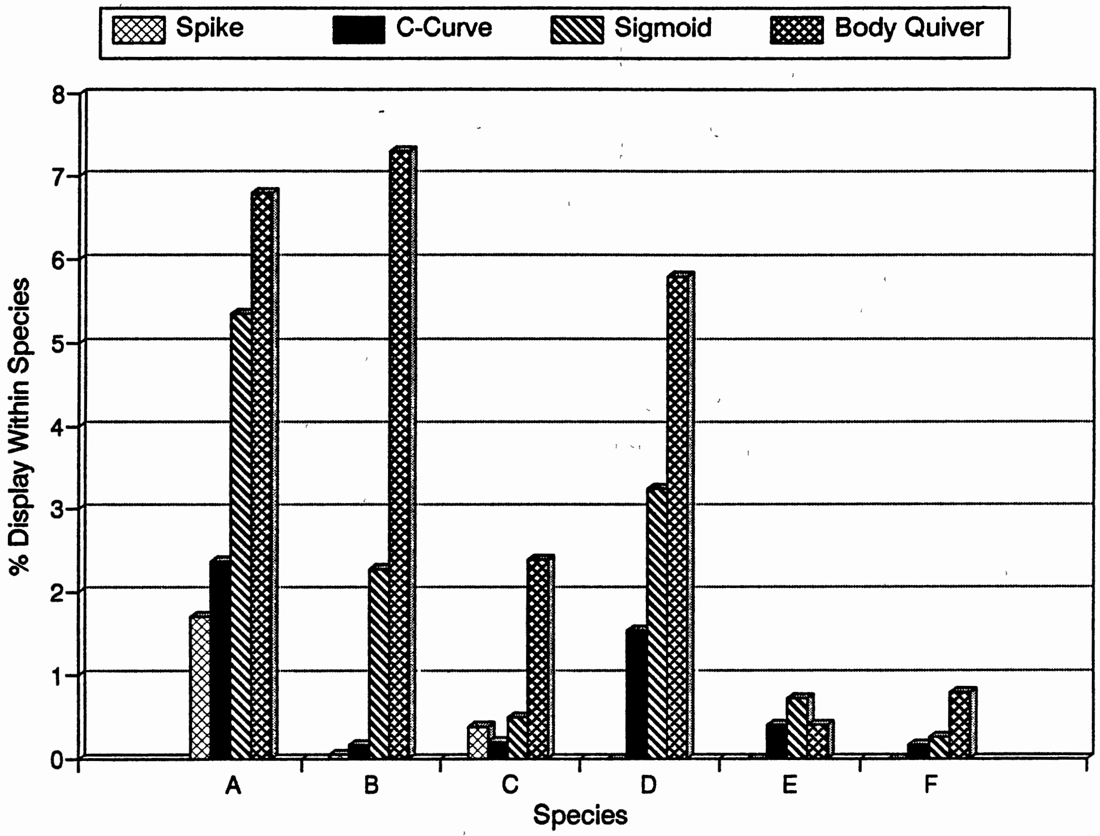


Figure 11. Relative Frequency for each species of full body displays. Species: (A) *C. acutirostre*, (B) *C. kingsleyae*, (C) *C. oxyrhynchum*, (D) *C. ansorgei*, (E) *S. capensis*, (F) *A. testudineus*

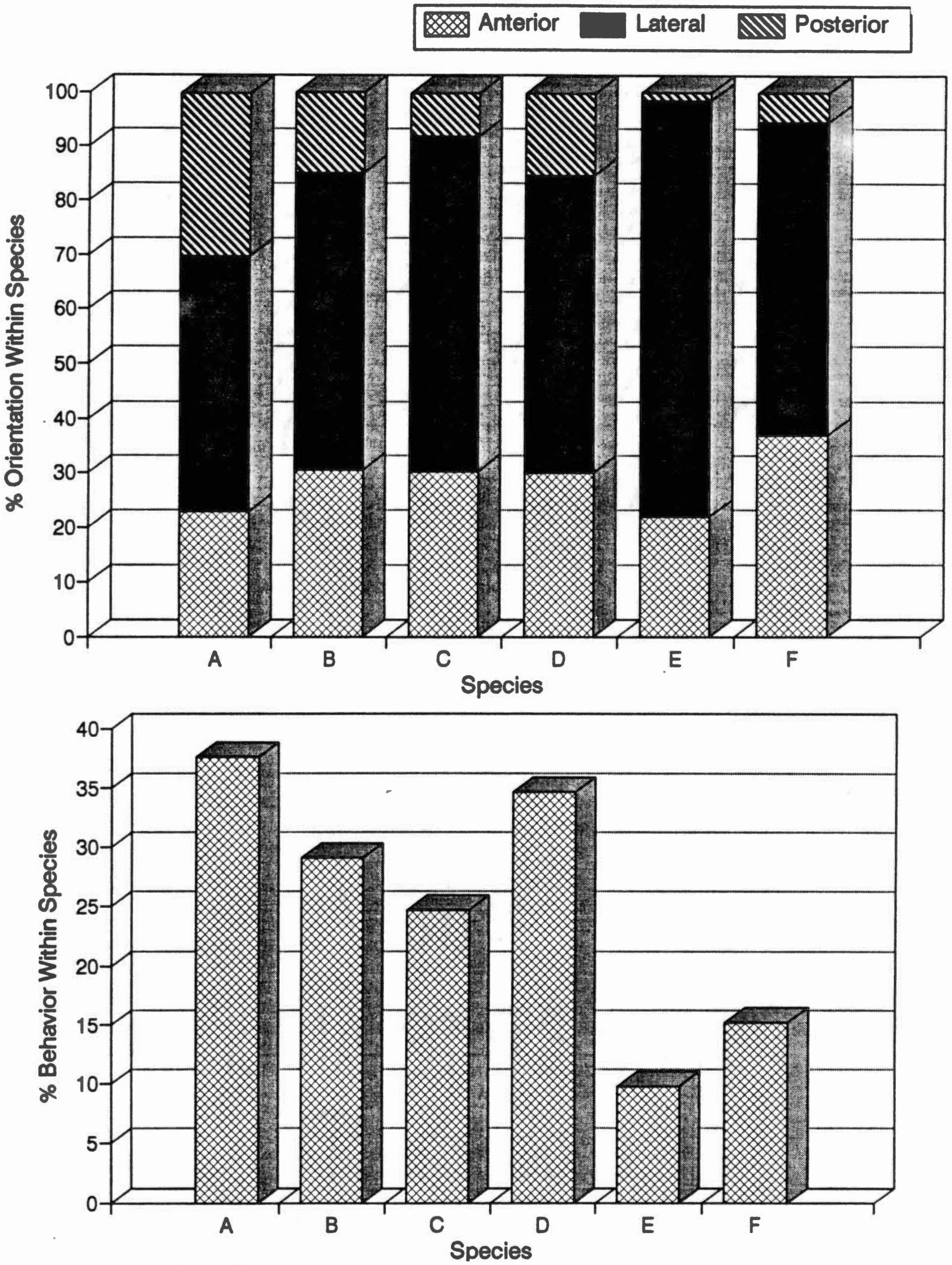
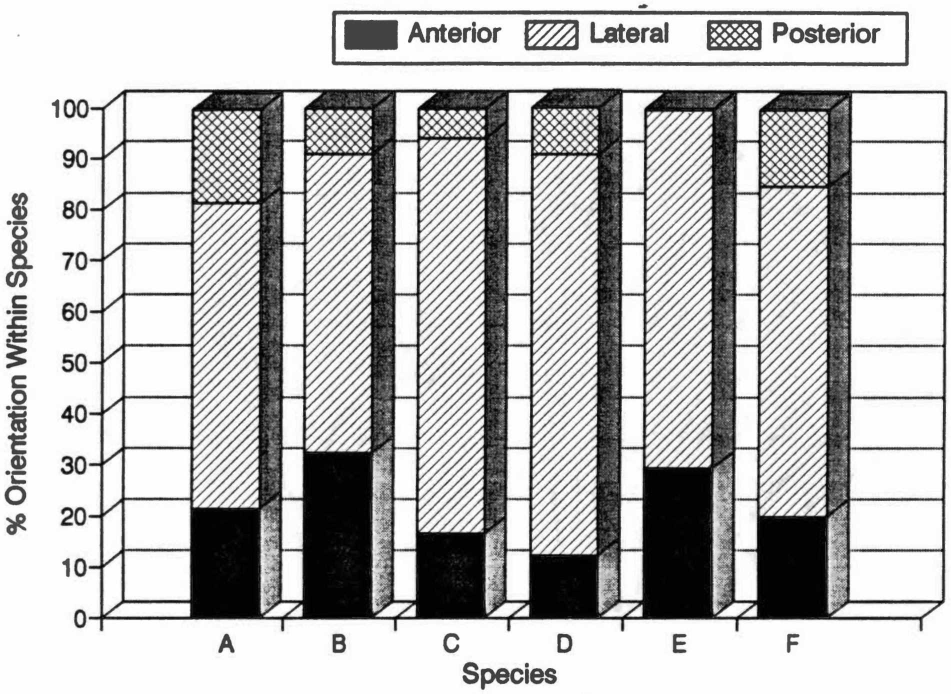


Figure 12. Top: Relative frequency for each species of Lateral Displays using each orientation. Bottom: Relative frequency for each species of LD. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*



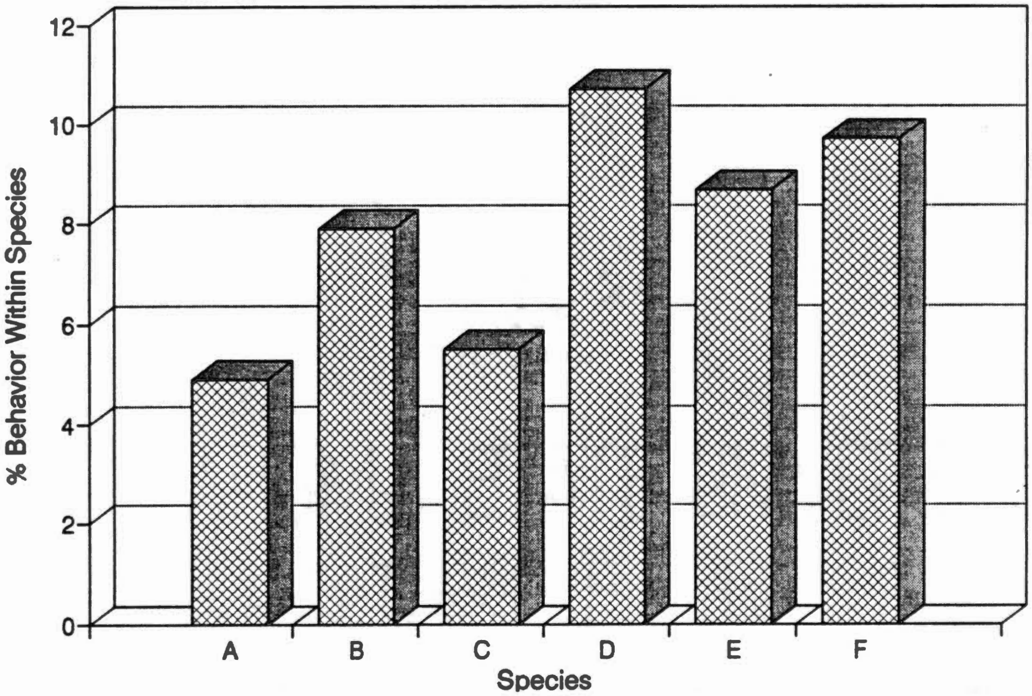
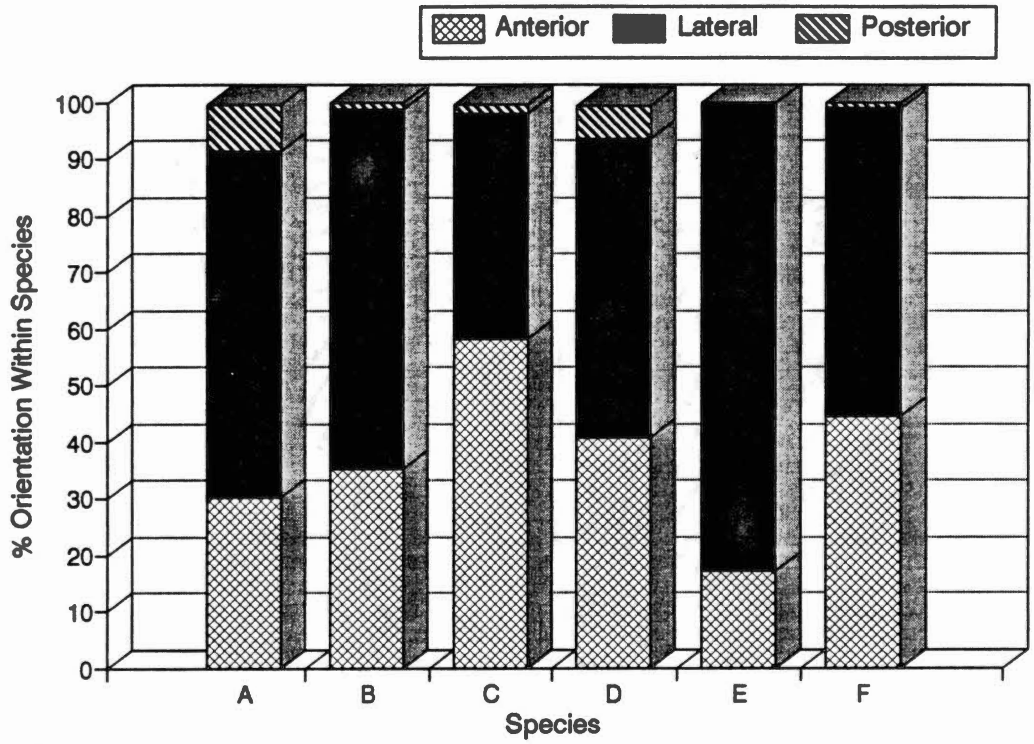


Figure 13. Top: Relative frequency for each species of Frontal Displays using each orientation. Bottom: Relative frequency for each species of FD. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*



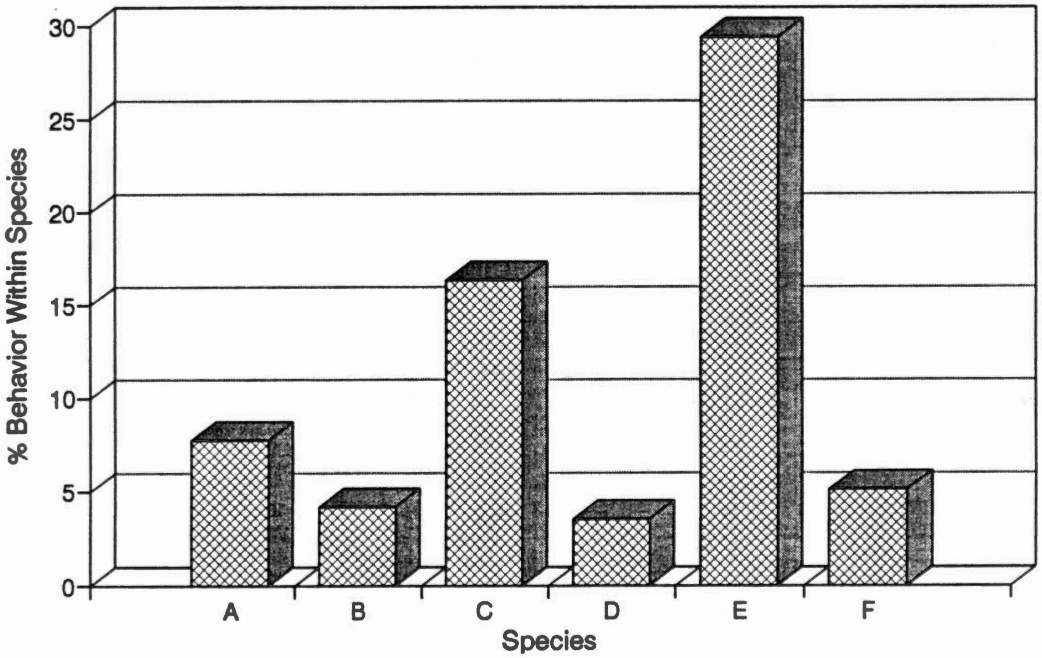
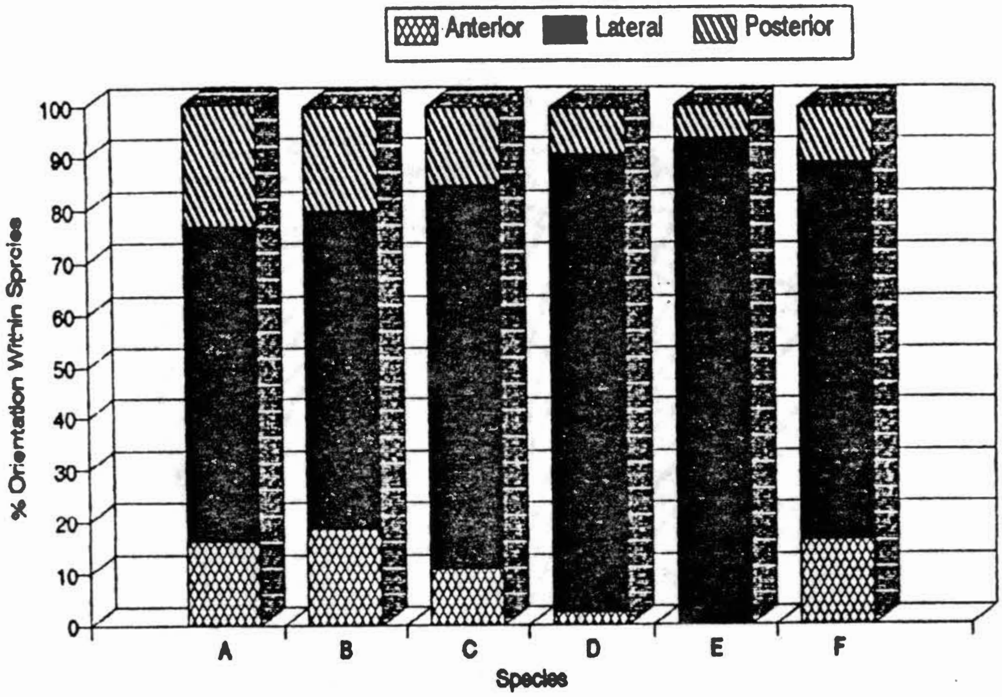


Figure 14. Top: Relative frequency for each species of Lateral Presentation using each orientation. Bottom: Relative frequency for each species of LP. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*



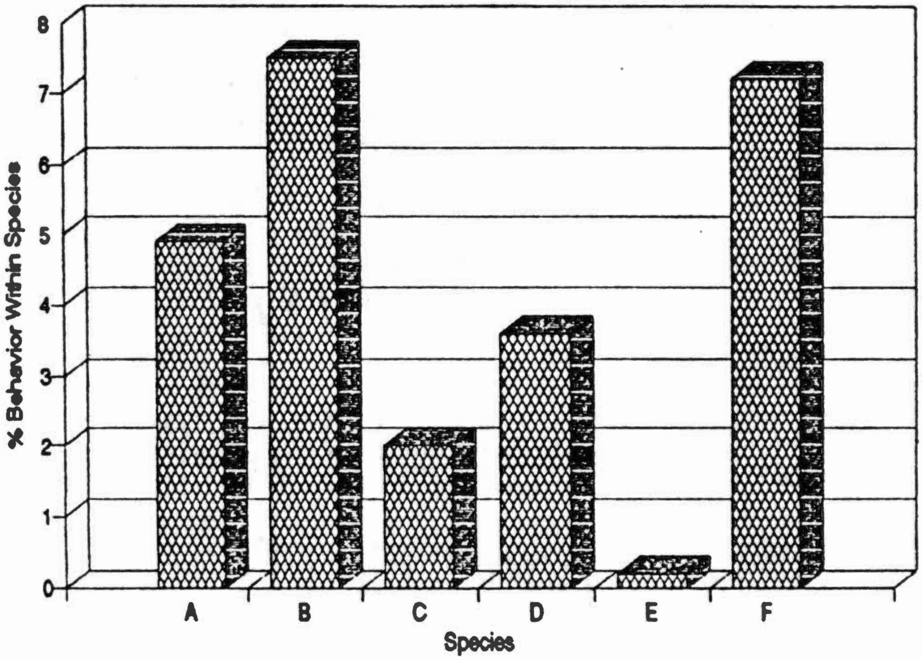


**Figure 15.** Top: Relative frequency for each species of frontal Approaches using each orientation. Bottom: Relative frequency of Fapp for each species. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

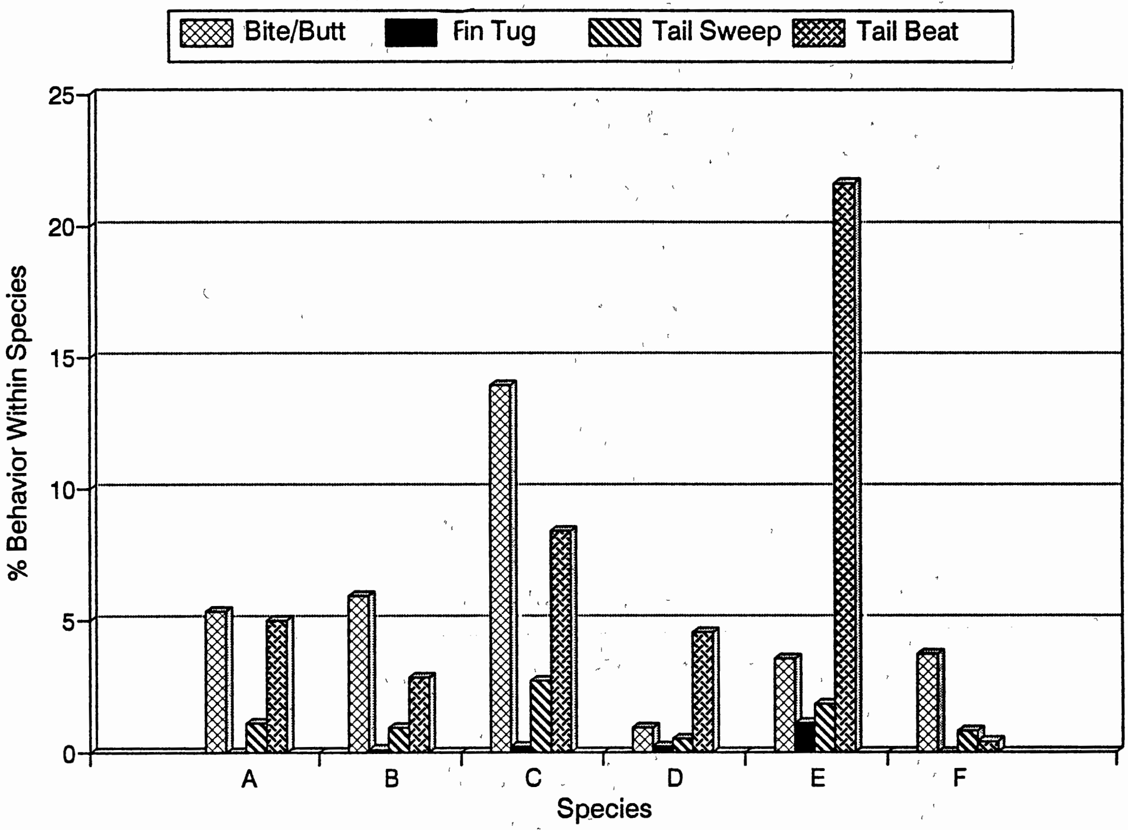


Figure 16. Relative frequency for each species of overt agonistic behaviors. Species: (A) *C. acutirostre*, (B) *C. kingsleyae*, (C) *C. oxyrhynchum*, (D) *C. ansorgei*, (E) *S. capensis*, (F) *A. testudineus*

of the opponent (Fig. 17). This orientation is consistent with the above discussed high frequency of lateral orientation while using other displays. Tail Beating orientation was variable and unpredictable. Interestingly, *C. acutirostre* and *C. ansorgei* were the only species studied to use the Caudal/Caudal orientation (Fig. 18). They were also the most frequent users of the SBTOF approach (Table 5). If both fish swam backwards toward each other with this approach form, positioning was appropriate for Caudal/Caudal Tail Beating. In the population tanks, both species were frequently observed in plant cover, and backing into cover, and Tail Beating against plant material or other objects. During active fighting C. acutirostre also used Fin Tugging, usually of short duration, displaying a bias for the Anal fin (Fig. 19). C. acutirostre did not Mouth Fight (Fig. 20).

*C. acutirostre* fought at the bottom of the water column (Fig. 21) and stayed within three body lengths of each other during approximately two-thirds of the total bout time (Fig. 22). This species was not highly aggressive, and seemed to rely on visual displays and low disturbance displacement displays to resolve most conflict situations. It also exhibited extended latency to initiate agonistic behavior. The fish generally had stopped fighting and settled close together on the substrate before the 30-minute filming was

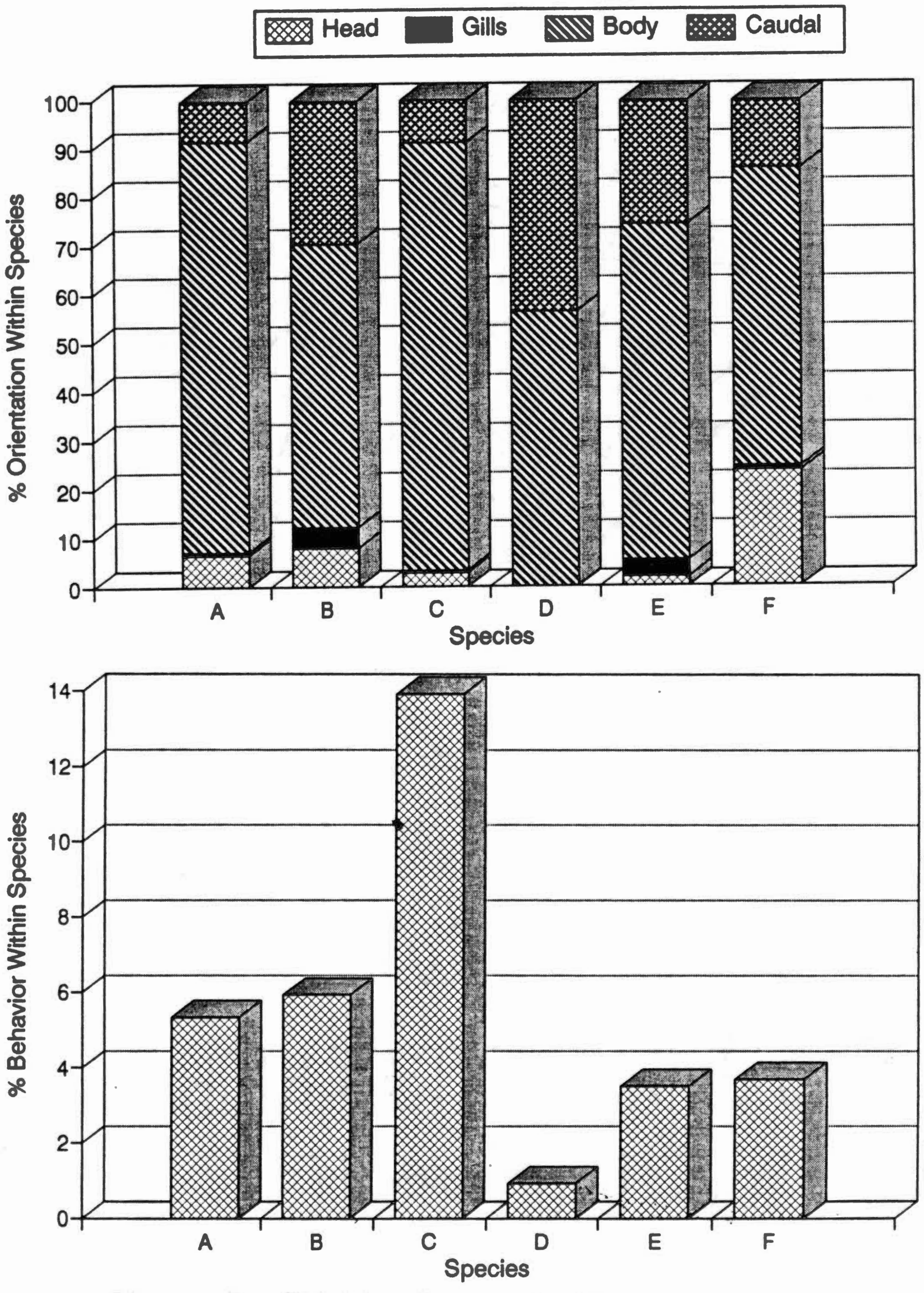


Figure 17. Relative frequency for each species of Bite/Butts to opponent's body. Bottom: Relative frequency of B/Bs. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

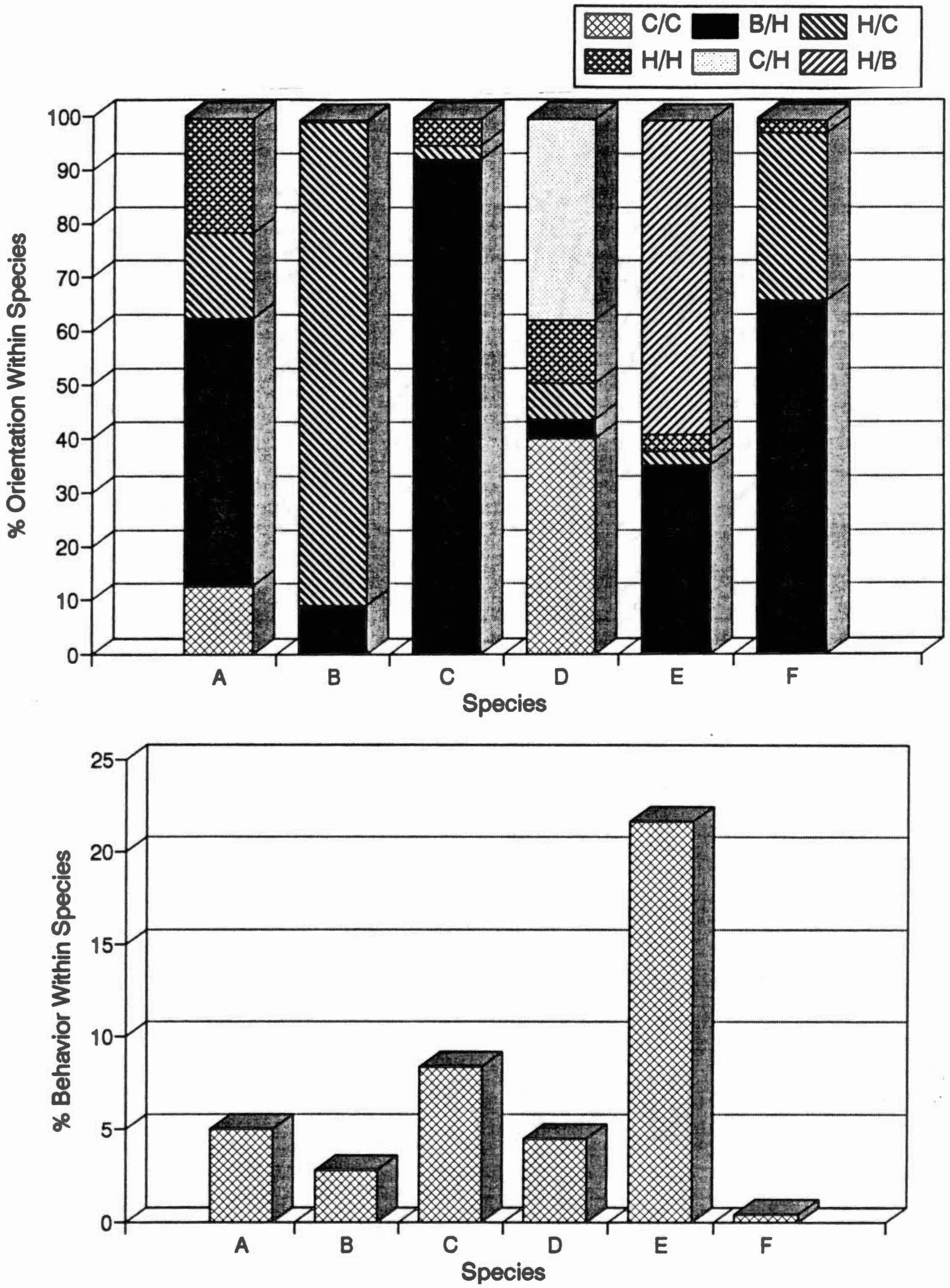


Figure 18. Top: Percent of Tail Beats, within species, using each orientation: C/C (caudal to caudal), B/H (body to head), H/C (head to caudal), H/H (head to head), C/H (caudal to head), H/B (head to body)
Bottom: Relative frequency for Tail Beats among species. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

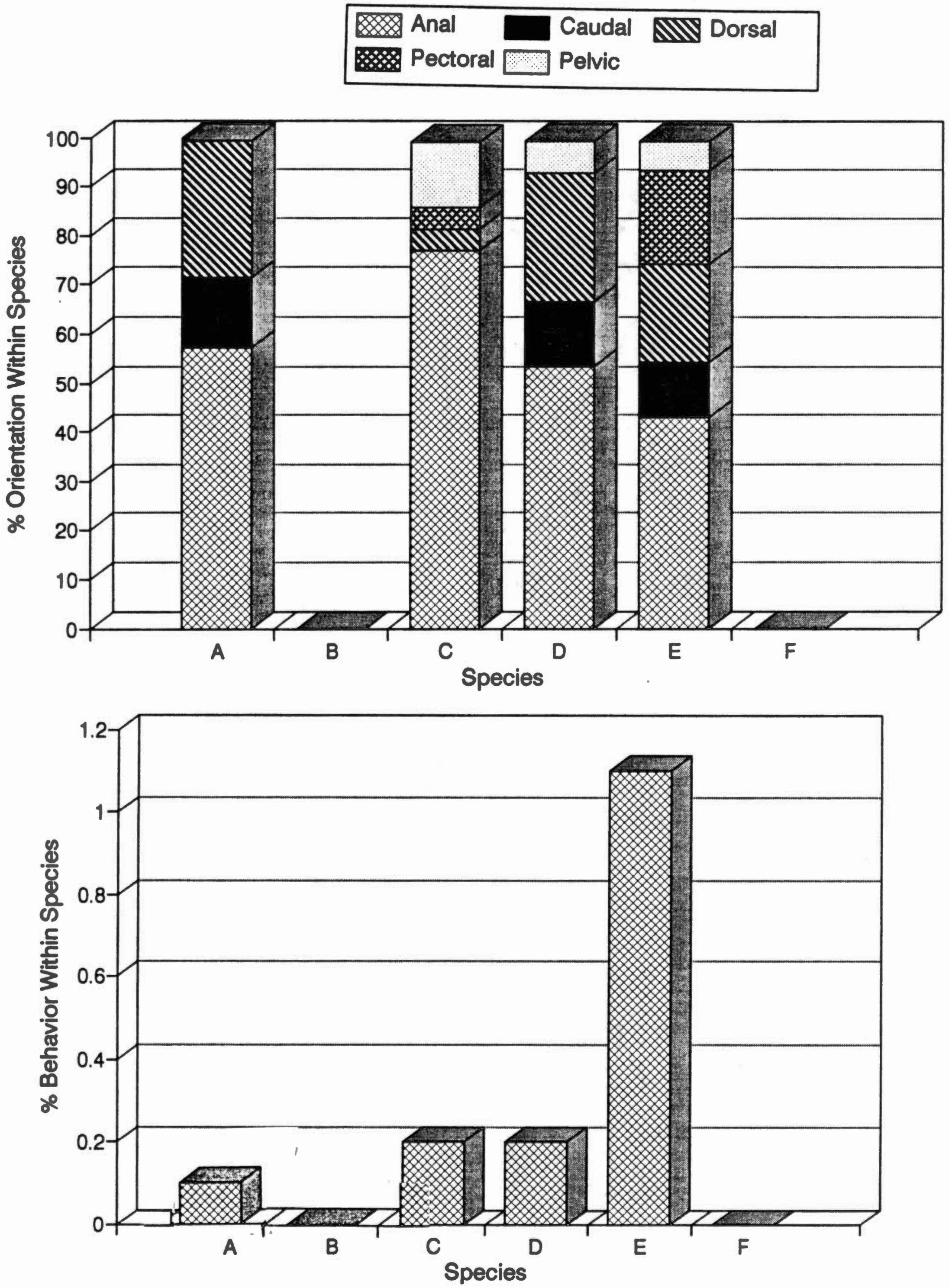


Figure 19. Relative frequency each species of Fin Tugs to each fin. Bottom: Relative frequency for each species of Fin Tugs Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

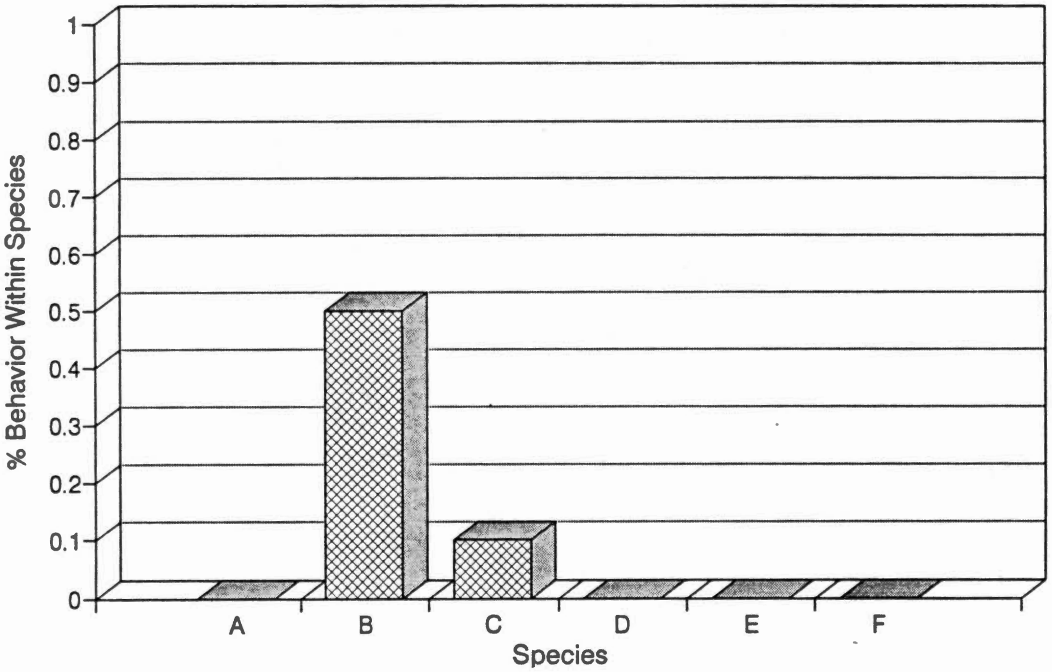


**Figure 20.** Relative frequency for all species of Mouth Fights. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

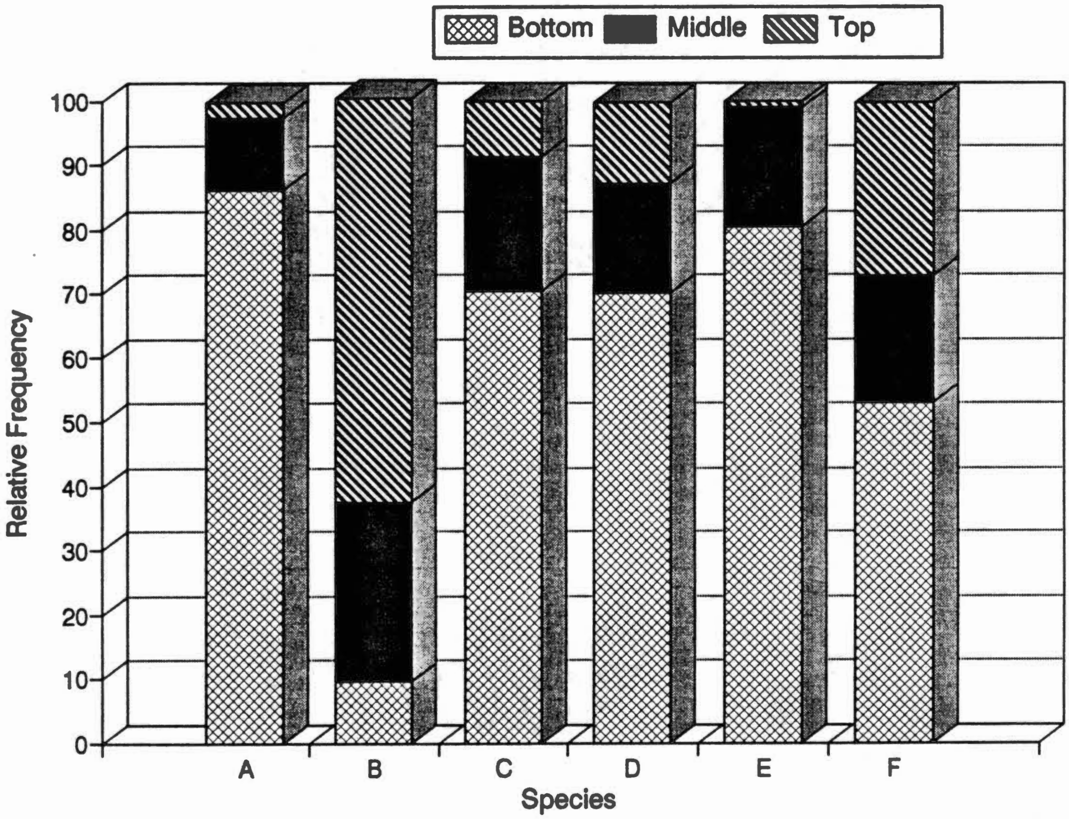


Figure 21. Percent of time for each species spent in three areas of the water column during the middle 20 minutes of each bout (time noted at two second intervals). Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

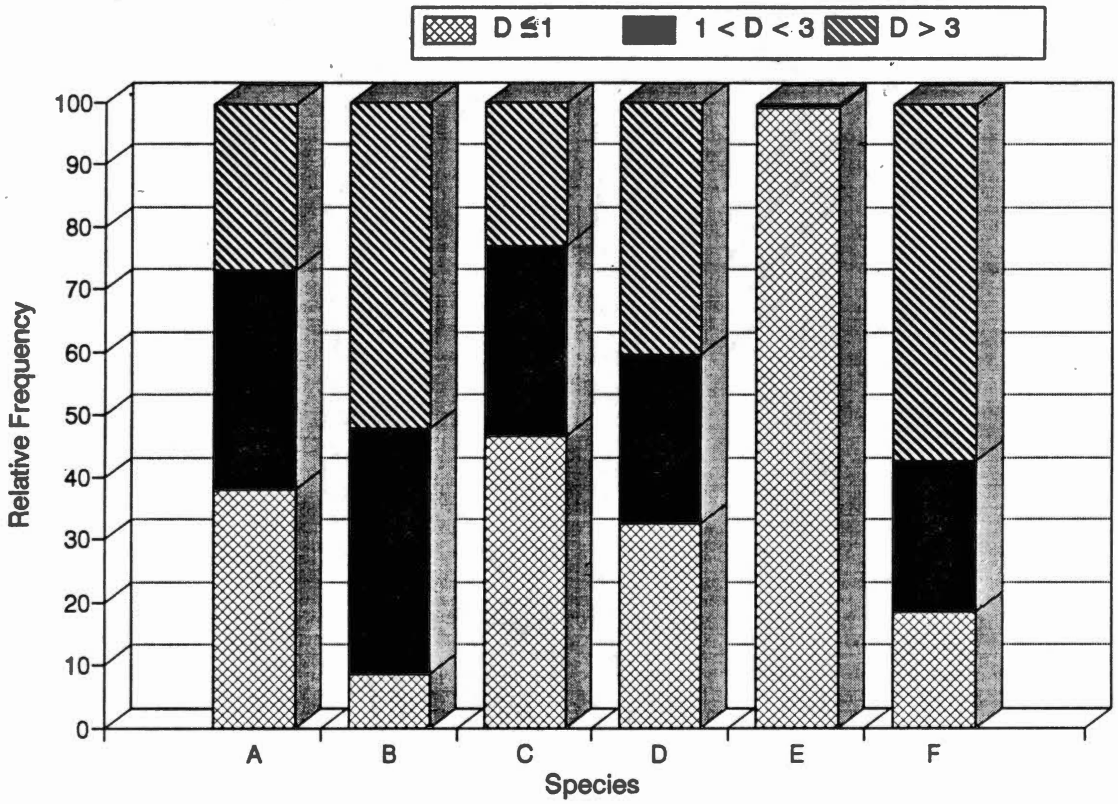


Figure 22. Percent of time for each species (noted at two second intervals) during the middle 10 minutes of each bout which fish spent at three relative distances apart (distance measured in body lengths). Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

completed. In population and community tanks they seemed to tolerate conspecifics in close proximity and did not inflict serious injury during bouts. However, these fish were aggressive, competitive feeders in the community tanks and would eat small fish, which eventually resulted in two classes: large healthy fish and small stunted fish. To prevent this, the smaller, less aggressive fish were removed and new population tanks established. These smaller fish did not perform well in agonistic bouts and their bouts were not used in the data set.

C. kingsleyae

This species occurs naturally in a wide variety of habitats including the turbid but open water of flooded areas (Pinter, 1984) and may be in frequent contact with conspecifics. In population and community tanks fish actively swam in open areas of the aquarium, seldom hiding, and larger fish maintained a defensible territory within the tank. Agonistic bouts occurred most often in the upper one-third of the water column (Fig. 21). In established populations, fish Chased and nipped at one another(Fig. 23), as if testing a dominance hierarchy. These encounters would escalate into Tail Beating and Bite/Butting episodes, yet the fish could be kept together safely. They appeared aware of general lab activity and did not seem to startle easily

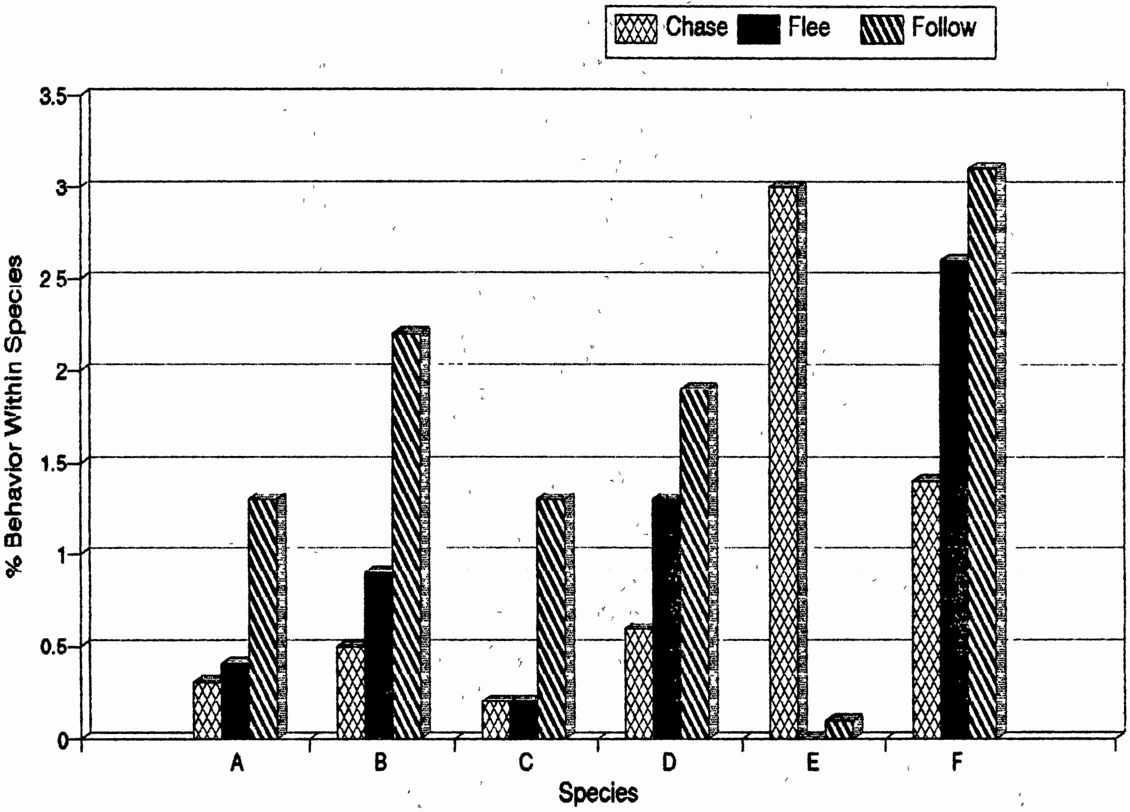


Figure 23. Relative frequency for each species of Chasing, Following, or Fleeing. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

(personal observation). C. kingsleyae were competitive feeders and this resulted in populations of fish of three general sizes. Each tank contained one or two large fish, several medium sized fish and one or two smaller fish. The first two size groups fought easily but the third, smaller, group were difficult to use for agonistic bouts.

While isolated by the partition for acclimatization to the bout tank, they appeared to establish territories. When the partition was removed, they swam in wide arcing circles, approaching from opposite ends of the tank, displaying at a distance, and returning to their respective ends of the tank. As one fish became more intrusive the resident fish Chased the intruder and continued to display. These standoffs were repeated several times, until the intruder did not Circle away. The fighting then escalated to Tail Beating, Mouth Fighting, and Bite/Butt encounters. C. kingsleyae did not remain close together for long periods during bouts (Fig. 22). Instead, they Circled (Fig. 24) and orientated for a Frontal Approach, with a bias for approaching the lateral portion of the opponent's body (Fig. 15). The Frontal Approaches were often direct and rapid, incorporating a Gular Flair and Opercle Spread, terminating in a Bite/Butt sequence, Frontal Display, or an Avoid (Table V). Whenever a fish used an Avoid, it Circled away and Body Quivered. Often the approached fish stopped swimming and Body Quivered as the opponent drew nearer. Body Quivering

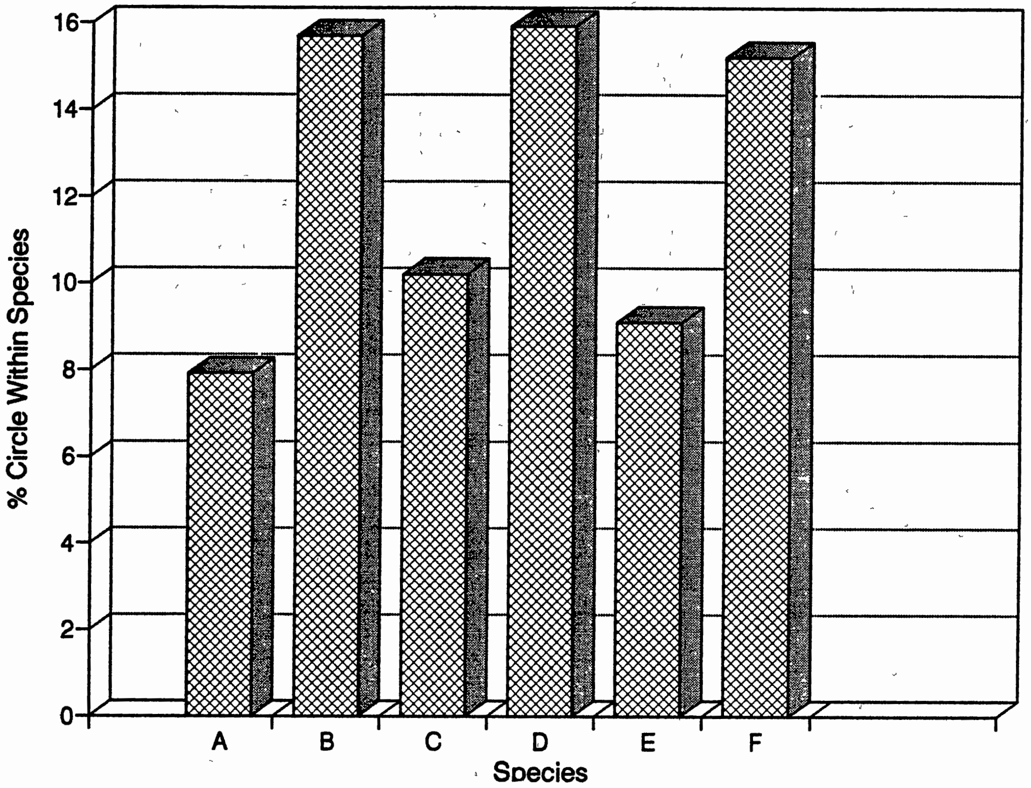


**Figure 24.** Relative frequency of Circles for each species. Species: (A) *C. acutirostre* (B) *C. kingsleyae* (C) *C. oxyrhynchum* (D) *C. ansorgei* (E) *S. capensis* (F) *A. testudineus*

was relatively more frequent in *C. kingsleyae* bouts than in those of the other species studied (Fig. 11). Relative frequencies of Lateral Displays, Lateral Presentations, and Frontal Displays were not significantly higher than in other species, but approximately one-third of these displays were presented anterior to the opponent (Figs. 12, 13, 14) and included a Sigmoid curve with a relative frequency second only to *C. ansorgei*.

*C. kingsleyae* presented a larger proportion of its Frontal Displays anteriorly than any of the other species studied. This consistent pattern, and the significantly high frequencies of the Frontal Approach and Mouth Fighting (Table V) reflect a general pattern of frontally oriented agonistic behavior. These fish have white areas on the maxillary and the distal edge of the opercle; areas of the premaxillary also become white as the fish matures as well. The white areas are distinctive against the dark background of the fish's head and become more distinct as the fish ages. These prominent markings may increase the impact of the frontal view in turbid water and/or play a role in maintaining the observed loose dominance hierarchy. During a bout these normally slate gray, non-patterned fish often appeared mottled with numerous iridescent vertical lines on the body. The fish also could reverse the normally dark color and dark caudal spot pattern to appear a light silver grey with a white caudal spot; however, no positive relationship of color pattern and dominance was established.

Tail Beating in this species consisted mostly of Head/Caudal reciprocal fighting (Fig. 18). Other fish used this orientation, but C. kingsleyae was the only species in which each beating movement was reciprocated. The fish approached frontally, aligned head to tail, circled together and began Tail Beating, generally exchanging 3-5 beats. C. ansorgei also used this orientation, but during the exchange of beats, they typically went into prolonged Fin Tugging, while C. kingsleyae did not use Fin Tugging (one Fin Tug was recorded). Bite/Butting to all four qualifying areas of the opponent was observed in this species (Fig. 17). Most attacks were directed at the lateral body area, which is consistent with the high proportion of lateral Frontal Approaches (Fig. 15). The relatively high proportion of Bite /Butts to the gills and head are possibly a result of the general anterior orientation for displays. Caudal Bite/Butts in general occurred after the conflict was resolved and the dominant fish Followed the subordinates (Fig. 23), repeatedly nipping at the caudal region. This behavior continued until the fish were separated. The duration of this Chasing, Following, and Caudal Bite/Butting probably was an artifact of fighting in a confined area.

Mouth Fighting was relatively frequent in this species (Fig.20) and presented in a unique, apparently highly ritualized form. The fish oriented face-to-face with the mouth open and then snapped the mouth closed. The snapping motion of one fish forced the opponent backwards, then that fish swam forward and snapped its mouth, forcing the original actor to retreat This snapping motion was repeated by both fish several times. Eventually one fish Head Jerked (Table V) and swam away, the dominant fish Body Quivered then swam away (Fig.11). Though C. *kingsleyae* often continued fighting the entire 30-minute bout without conflict resolution, neither fish had shredded fins or missing scales.

C. kingsleyae seem to have evolved a highly ritualized repertoire of agonistic behaviors which allow frequent interactions without serious injury. Body markings and patterns intensify as the fish mature, which may augment opponent appraisal, intention signalling and the establishment of dominance hierarchies or territoriality.

### C. *oxyrhynchum*

This cryptically marked species often hid in plant cover on the bottom of the aquarium but was not as elusive in the tank as *C. acutirostre* or *C. ansorgei*, nor as active in the open water as *C. kingsleyae*. It was more active in the evening when lab activity was at a minimum, but did spend part of the day in open areas of the tank.

These fish periodically defended areas within the population and community tanks, but did not do so as frequently as C. kingsleyae. The well-marked pelvic fins were flashed and the darkly outlined caudal fin rippled because the fish seemed to rely on visual signals in the big tanks. C. oxyrhynchum were not aggressive or competitive feeders in the population tanks and the individuals from one shipment grew uniformly so that all specimens were within a few millimeters in size.

It was not difficult to stimulate agonistic behavior between them although they were sensitive to being moved from tank to tank and were allowed longer periods for acclimatization in the bout tank, than the other species, before the partition was removed. Upon removal of the partition, each fish stayed in its area of the tank, rested on the bottom, faced the other fish and raised and lowered the dorsal fin. Eventually, one fish would slowly swim toward the other, stop, Spike Display, and swim forward again. Once contact was made between the fish, the fighting escalated to Tail Beating, Bite/Butting (Fig.16), and the displacement patterns of SSTOF, SUB, and SOB (Fig 10). Most of the fighting occurred in the bottom one-third of the water column (Fig. 21). The fish continued to fight with infrequent separations, seldom moving more than three body lengths apart (Fig. 22). C. oxyrhynchum bouts were active, with the highest relative frequency of major behaviors of all species studied in the Ctenopoma genus (Fig. 9).

Mouth Fighting was relatively frequent (Fig. 20) and prolonged within these bouts (Fig. 20). With mouths clamped together, the fish used strong undulations of the tail and body to snap the opponent's body. These episodes appeared to be tests of strength and endurance. The fish which broke away from the hold would be Chased and subjected to a series of Bite/Butts on the body. C. oxyrhynchum used Bite/Butting significantly more often than the other species (Table V), and showed a bias for attacking the lateral area of the body (Fig. 17), even to inflicting injury (loss of scales) on the ventral areas of the opponent's body. Lateral Presentation was used more often than in the other Ctenopoma (Fig. 14). When Laterally Presenting, the fish would SSTOF and Lean on the opponents head (Fig.10), pushing it down. Often the opponent would Bite/Butt the leaning fish; if this happened, the presenting fish began a Tail Beating sequence (Lean, Tail Beating, SSTOF). This sequence continued until the opponent turned and swam away or swam under the body (SUB) of the leaning fish (Fig. 10). If the opponent managed a SUB, it would Tail Sweep the other fish (Fig. 16), do a Lateral Presentation and the sequence would start over with the fish having reversed roles. During intense fighting, the fish swimming under the body grabbed the anal fin or pelvic fin (less often) and Fin Tugged (Fig. 19). The propensity for this complex sequence of behaviors in the agonistic repertoire of C. oxyrhynchum is reflected in the statistically significant frequencies of the Lateral Presentation, Bite/Butt, Tail Beat (B/H) , Tail Sweep, and SUB (Table V). This ritualized sequence of events appeared to be a test of strength: if the opponent could not maneuver a SUB, it would no longer Bite/Butt the presenting fish and allowed itself to be displaced. C. oxyrhynchum did not frequently use the low disturbance C-Curve or Sigmoid Curve in their displays (Fig. 11).

C. oxyrhynchum lived well together in the population and community tanks. They used visual signaling in the more complex environment of those tanks and resolved conflicts with minimum contact. They seemed to rely on cover or retreat areas to reduce conflict.

C. ansorgei

These small fish with elongate bodies and ornate fins stayed hidden in the plants of the population tanks, with their dorsal margins touching the undersides of leaves. They were not hesitant to feed but soon returned to cover. They displayed and nipped during feeding, and food competition resulted in three size classes similar to those in C. acutirostre. All C. ansorgei were less than 15 cm. SL. when we received them and were maintained for several months before bouts could be staged. During agonistic encounters these pale, thin fish developed intense color patterns: six to eight black vertical bars separated by bright orange areas on the body and median fins. The caudal fin became solid black and the pelvic fins black and orange with a white anterior edge. This dramatic color change was accompanied by flaring the long medial fins, extending of the pelvic fins, and spreading of the caudal. Both fish assumed this color pattern and apparent size increase during the conflict. Whenever two fish were fighting in the population tank, others would approach and assume the fighting color pattern. It was possible to have two or three pairs fighting at the same time, because those watching the first conflict would become involved. This situation was common if a new fish was added to the tank. I did not observe these spontaneous bouts escalate to Fin Tugging, and the fish were not injured during these fights.

Staging agonistic bouts was difficult with this species. They would not fight in the large tank that had been used for the other Ctenopoma bouts. The fish would not approach each other, staying at opposite ends of the tank after the partition was removed. I isolated 12 fish (four of each size group) in quart jars which had been painted black, keeping the fish isolated a minimum of three days. When both fish were simultaneously placed into a smaller bout tank, which had three opaque sides, fighting usually occurred within minutes. This species was territorial in population tanks, with larger fish occupying and defending favored spots. Smaller fish crowded into areas with poor cover and the mid-sized fish hid individually in any space available. Territories were centered around plant and rock cover and the lack of cover in the bout tanks may have increased the difficulty in staging bouts. If there was a size discrepancy of a few millimeters, the fish would not fight. Instead, the larger fish would Chase the smaller and shred its fins (Fig. 23).

Once bouts were initiated, these fish were highly aggressive and sometimes inflicted serious injuries, as fins were shredded and scales torn away. Displays contained full median fin spread, Gular Flair, and Opercle Spread. This species had the highest relative frequency of Frontal Displays (Fig. 13) among Ctenopoma species (Fig. 1). The display was used most often with a lateral orientation to the opponent (Fig. 13). C. ansorgei used the Sigmoid curve more than other species and was second only to C. acutirostre in use of the C-Curve. They also frequently used Body Quiver (Fig. 11). Fin Tugging was used by this species, and although they were not the most frequent Fin Tuggers (Fig. 19), each tug was prolonged and more time was spent tugging than in the other species. Each time the tugging fish clamped on to a fin, it was dragged around the tank by its opponent. At times the pair would rest on the gravel with the tugging fish lying on its side under the opponent. C. ansorgei and S. capensis were the only species which used Fin Tugging in this manner: all other species which used Fin Tugging grabbed the fin and jerked the head laterally several times and released the fin. C. ansorgei oriented parallel and laterally, head to tail, and began to Carousel, each fish trying to grab an anal or dorsal fin (Fig. 19) while protecting its own fins from the opponent. Carouseling behavior was not seen in the other species (Table III). The fin tugging was often reciprocal, perhaps a test of strength or endurance, with the winning fish performing the last Fin Tug. This species also exhibited Arrow display, which was unique to the species (Table III). Arrow, seemed to be an appeasement behavior although it was seen being used simultaneously by both fish.

Visual display is important in the development of a social system in this species. Territoriality is superimposed on a dominance system related to size, though the social hierarchy might not be so prominent in nature where space is not limited. This predominance of visual displays is consistent with the bright coloration and large fins that enhance apparent size increase; prolonged Fin Tugging might test for resource holding power. C. ansorgei spent as much time more than three body lengths apart as they did close together (Fig. 22). They often showed distance displays, then swam close for tactile displays, and swam apart again. If there was a size discrepancy, they used visual displays for several minuets, and the larger fish Chased the smaller and nipped its caudal fin. If there was not a size discrepancy, but the conflict was resolved, the match would end in the same manner. C. ansorgei could be safely maintained in the complex environment of the population tanks, resolving conflicts without injury. The intensity of fights in the confines of the bout tank, which offered no retreat, might indicate that the species has evolved social and agonistic behaviors that allow living in groups but has not evolved inhibitory mechanisms to prevent injury when forced into extended close contact.

### S. capensis

A mountain stream species endemic to temperate waters of South Africa, these fish were aggressive and had to be kept isolated. Obtaining live specimens from South Africa was extremely difficult. Soon after arriving some of the 20 small fish began to die with an unknown bacterial infection. After they were finally stabilized, only ten fish survived. These fish were shy in the lab and hid behind plants during the day. Initially, I tried to stage the S. capensis bouts by isolating the fish in the bout tank with a partition. However, they managed to get around the partition during the night, and one fish was killed while the survivor was severely injured. Because of the small number of live specimens and the possibility of further loss from avoiding the barrier, fighting protocols were modified. S. capensis were simultaneously placed in the bout tank and an assistant started the film and clock. The fish immediately began to fight, and the contrast between the light background of the body and dark body stripes intensified. Since they were maintained in individual ten-gallon tanks, isolation conceivably could have contributed to the lack of inhibition to fight. General activity level during a bout was highest of all species studied (Fig. 9). Most pairs were still fighting when the scheduled bout was over. Fish were immediately separated when the 30-minute bout was finished to prevent unnecessary injury.

The fish were close together during most of the bout in this species (Fig. 22), approaching with the SSTOF and Leaning against each other (Fig. 10). They used Frontal Approach less than any species studied (Fig. 15) and rarely used full body displays (C-Curve, Sigmoid, Body Quiver), which seemed to be primarily distance displays (Fig. 11). This close proximity correlates positively with the large ratio of Lateral Presentations to Lateral Displays (Figs 12, 14). Pairs aligned laterally and parallel, head to tail, each fish positioning its opercles even with or just slightly posterior to the opponents' opercles. Each fish swam forward or backward using the pectoral fins to maintain this position and prevent the opponent from executing a SUB or a Fin Tug. The opercles of this species are marked with broad, dark stripes radiating posteriorly from the eye which may intensify the visual impact of the Opercle Spread. *S. capensis* alone used the Head/Body Tail Beat (Fig. 18) which presented the Opercle Spread close to the opponents' head while undulating the body and caudal area strongly. These powerful beats slammed the head into the opponents' body. Lateral portions of the bodies of both fish were injured during these Tail Beat episodes. Unlike *C. kingsleyae*, which reciprocated each beat, *S. capensis* reciprocated each sequence of beats. *S. capensis* used the Tail Beat and Fin Tug more than the other species (Fig. 16). They grabbed any fin, with a slight bias for the anal fin (Fig. 19), and tugged it several times, often shredding the fin. They occasionally held onto a fin and were dragged around the tank by the opponent. These aggressive fish were not observed Mouth Fighting (Fig 20) and used the Bite/Butt with relatively low frequency (Fig. 20). Often, Bite/Butts appeared to be unsuccessful Fin Tug attempts, but they were violent and frequently resulted in the removal of scales. Pairs remained close to the bottom of the tank during most fights (Fig. 21) and would Circle with a Spin to realign to the lateral opercle to opercle position whenever necessary.

This geographically isolated species does not seem to have inhibitory behaviors that allow close contact with conspecifics without serious injury. The relatively small space available in the aquaria may have increased the aggressive tendencies of these fish.

### A. testudineus

Known as the Asian Climbing Perch, A. testudineus live in varied aquatic habitats including brackish water (Pinter, 1984). They are strong jumpers, jumping through any crack in the aquarium coverings, and were difficult to maintain. Small populations (four or five fish) of similar sized fish worked best. They did well in community tanks if small numbers of conspecifics were kept together; otherwise they jumped out. Stimulating agonistic behavior was difficult, and unless crowded, the fish would not fight. Bouts were staged in the same small opaque tank used for C. ansorgei, with a slight modification to tightly fit the tank cover. This modification prevented fish from jumping the partition and leaving the bout area. At the beginning of the bout both fish tried to jump out, and if they were not of equal size, the smaller fish continued the attempts. Whenever a conflict was resolved, the loser attempted to jump out.

A. testudineus have an iridescent olive to gray body, dark caudal spot, small dark spot on the posterior edge of the opercle, and clear fins. They do not have stripes or markings on the fins or body that would enhance displays. They resembled C. kingsleyae in the use of open water, fighting distance (Fig. 22) and frontal orientation for many of their displays. A. *testudineus* used Frontal Approach (Fig. 15) with the second highest relative frequency, just slightly less than C. *kingsleyae*, and they were second only to C. *ansorgei* in the use of Frontal Displays (Fig. 13). They did not have a high relative frequency of Lateral Display or Lateral Presentations but frequently used an anterior orientation during these displays (Figs. 12, 14).

These fish initially positioned themselves as far apart as possible, one fish in a bottom corner and the other in the opposite top corner. They swam across the tank, interacted, Circled (Fig. 24) in wide arcs and returned to separate corners. Usually one fish Followed or Chased the other back to its respective corner (Fig. 23). They were "hit and run" fighters. They approached the opponent, executed a single Bite/Butt or Tail Beat and quickly retreated. Bite/Butt was the most frequently used overt behavior (Fig. 16) although they used overt behaviors less frequently than the other species (Fig. 16). A. *testudineus* did not Mouth Fight (Fig. 18).

Surprisingly, they did not use the full body displays (Fig. 11), which should be effective at middle and greater distances and were frequently used by C. *kingsleyae*. However, A. *testudineus* did use two unique motor patterns, Digging and Shimmer (Table III). Digging was used during intense fighting whenever a fish was approached. Other species used Sigmoid curve and C-curve in this situation.

Digging was frequently used in displacement situation by both fish during intense conflict and seemed to be an appeasement behavior used by the loser after conflict resolution. On two occasions (not during bouts) A. testudineus was observed burrowing into the gravel (using the typical Digging movements) when startled. Shimmer appeared to be a modification of Body Quiver, with slightly larger body oscillations and a Lean that oriented the lateral portion of the body toward the opponent. The Body Quiver appeared to be performed with disregard for the position of the opponent, but Shimmer was performed for the opponent. If a Following fish slowed, the leading fish stopped and Shimmered; or a Circling fish would stop and Shimmer in front of the opponent before swimming back to its corner. Shimmer as with Body quiver, often followed an overt attack. A. testudineus used Body Quiver and Shimmer movements, and the function seemed to distinguish the behaviors as easily as the action patterns.

A. testudineus were not aggressive and seem to have evolved strong inhibitions against fighting. The close quarters of the bout tank created an environment that precipitated some agonistic behaviors which, in nature, probably would have been avoided.

# CHAPTER V

## DISCUSSION AND CONCLUSIONS

Evolutionary relationship (taxonomic affinity) has traditionally been divined by the presence, in two or more taxa, of specialized traits, or synapomorphies, which are absent in other, presumably more distinct taxa. Although the construction of hypotheses of relationship (phylogenies) has been strongly biased toward the use of morophological characteristics, taxonomists have increasingly been attracted to the use of non-morphological traits for assessing such relationships. Whitman (1919) was perhaps the first to suggest that instinctive behaviors had to evolve in much the same ways that structural features evolved and that behavioral similarities were reliable indicators of close relationship. Lorenz's (1941) elegant analysis of the behavior of Anatine ducks probably had the most influence in convincing scientist that procedures for such analysis could be worked out practically. The principle was established, and most comparative ethological studies conducted over the last fifty years have had as their goal elucidation of how behavior might have evolved in a group of species. Working out how similarities of movement patterns might suggest phylogenetic affinities has been a less common objective.

The fundamental problem, of course, lies in the fact that very similar behaviors (or structures) might arise in distantly related species (convergence) while elements of an ancestral behavior pattern may easily be drastically altered or even omitted completely in one or more descendant species. Although this problem is inherent to all phylogenetic analysis, it is particularly troublesome when using behaviors as character states because of their ephemeral nature, the number of parameters (form, frequency, and intensity of movement) that can be altered to completely change the appearance of a movement, and the obvious potential for experiential (learning) or environmental factors to alter a movement pattern during ontogeny. When Atz (1970) and others pointed out these difficulties, ethologists showed that many behaviors were not only highly stereotyped, but also very conservative. These hard-wired "instinctive" behaviors, often comfort movements or body care activities, remained remarkably constant among members of an obviously affiliated species cluster. There has been relatively little discussion or study of whether all stereotyped behaviors exhibit such conservatism, or whether plasticity (pliability in an evolutionary sense) varies among different functional classes of "instinctive" behaviors.

Especially in the case of signal behaviors (displays) in fish, where diversity of movement is constrained by the dense water medium and the limited physical equipment (fins, and strongly metameric musculature) the opportunity for striking change in a movement pattern at relatively low "cost" in terms of physiological or morphological alteration is extremely high. For example, previous studies on fishes have almost invariably recognized a behavior in which a fish spreads its median fins, and sometimes the pelvics, and aligns itself in front of, or beside another fish during fighting or courting sequences. These "lateral displays" or "lateral spreads" have typically been treated as if they were one kind of behavior, despite the obvious variation in orientation components associated with their use. Perhaps because ethology realized early on that many such orientation components were highly susceptible to environmental cues and modification by learning, they were rarely considered in comparative studies. In this study, in which precise data was obtained on orientation and body position, it became clear that each species had a particular pattern of use of the different forms of lateral spread.

At first glance there would seem to be no reason to believe that synapomorphic LD patterns might not indicate common ancestry, but problems are associated with such an assumption. First, there is no evidence that variations of a basic display, even though they exhibit species-typical patterning, reflect any fundamental differences in the information transmitted by the display. At some level, there would have to be differences in causation, if only in mechanisms integrating motor coordination of the different movements, but we can only guess at how such changes might occur during the evolution of new forms. Actually, if fish were saying the same thing, but in slightly different ways among the different species, we might be able to argue that orientation patterns arise almost randomly, and strong similarities might argue for recent common descent. Because the present study did not investigate motivation, it is impossible to even speculate meaningfully on this point.

A second problem lies in the great variations in size and shape that exist among the species studied. Miller and Miller (1970) suggested that such factors might underlie the canalization of behavior patterns in Asian Anabantoids, and presented some evidence to substantiate that contention. If this were an important factor the three deep-bodied Ctenopoma should be separable from the other three species, and should also show some degree of homogeneity among themselves. Such does not seem to be the case.

Finally, adaptation to a particular ecological niche strongly canalizes both morphology and behavior in fishes (Miller, 1978) and could influence the pattern of use of major display units and the orientation components that modify their appearance and coordination (qualifiers). In a separate study, responses to shelter types and location, food types and location, and general habitat use were investigated, and were found to be quite distinctive among the six species studied. Thus, although there is almost no information on ecology available in the literature on these species, it is possible to infer much about their behavior in nature and speculate on how physical and trophic constraints might have contributed to emergence of some of the patterns seen in agonistic contexts. In the discussion below, I will use Norris's hypothesis of relationship and assume that if behavior co-evolved closely with morphology, and both presented equally valid information on phylogeny, fighting patterns should be more similar within a taxon than between taxa. Since the data obviously do not show such a pattern, suggestions will be made about the possible influences of strong adaptations to environment that seem to correlate well with the patterns exhibited.

Norris used A. *testudineus* as an outgroup for the African Anabantoids in his phylogeny of the family. If agonistic behavior is useful in revealing phylogenetic relationships, this Asiatic genus should present a pattern which separates it clearly from the African genera. A. *testudineus* was the least aggressive species studied, with the largest number of significant differences in frequencies of major behaviors (Table V). It exhibited two unique behaviors, Digging and Shimmering (Table III). In the companion study Digging movements were used while bottom feeding, and its presence in fighting may represent a ritualization of a trophic adaptation. The general pattern of agonistic behavior and strong inhibition against fighting clearly did separate them from the more aggressive African fishes.

S. *capensis* is not only highly differentiated morphologically from *Ctenopoma spp*. but is the only African species exhibiting a disjunct distribution from them. Its presence in cool, clear upland streams also hints at major ecological difference. Norris (1987) attributed some of their unique structural traits, particularly the reduced labyrinth, to probable adaptations for this distinctive environment. The agonistic pattern of this species was most overtly aggressive of all species and revealed no inhibitions against fighting nor adaptations to prevent serious injury. Pairs fought intensely for the entire bout and seldom separated more than one body length. They displayed a unique orientation for Tail beating (H/B) and had the highest relative frequency of Tail Beats and Fin Tugs. This intense aggressiveness and its quantitative manifestations segregated this species from the others.

Establishing an aggressive axis with A. *testudineus* at one extreme and S. *capensis* at the other left the four *Ctenopoma* species clumped within the mid-range. Three of these species, C. *kingsleyae*, C. *oxyrhynchum*, and C. *acutirostre* are placed within the deep bodied *Monkengia* group (Table I) and in the phylogeny presented by Norris are separated into two clades by the single trait of protrusible jaws in C. *acutirostre*. The *Monkengia* group possesses a reduced labyrinth and should be less dependent on atmospheric oxygen than the *Ctenopoma* or *Nana* groups (Norris, 1987). Thus C. *kingsleyae* and C. *oxyrhynchum* should be most similar, with C. *acutirostre* showing slight dissimilarity. The fourth species, C. *ansorgei* is a sexually dimorphic bubblenest builder of the *Nana* group and should exhibit an agonistic pattern reflecting a more distant phylogenetic relationship incorporating more elaborate signalling behaviors.

Agonistic behaviors of the *Monkengia* species did not reflect the expected pattern. C. *kingsleyae* was the most dissimilar species with low frequencies for all overt attack behaviors except Bite/Butt. They also exhibited a modified Mouth Fighting which prevented injury and maintained a moderate distance between fish during fights. In general they seemed to stay distantly spaced, approach and exchange Bite/Butts or Tail Beats, and resume positions away from each other. Most fighting behavior took place at the top of the water column while C. oxyrhynchum and C. acutirostre frequented the bottom cover areas. C. kingsleyae inhabits the turbid open waters of the riverine flood plains most of the year, so the low aggressiveness and spacing patterns observed during agonistic bouts may reflect adaptation to movement and perhaps loss of a territorial social pattern.

C. oxyrhynchum resembled C. acutirostre in the use of the water column and in needing cover. but C. acutirostre stayed in intimate contact with plants while C. oxyrhynchum hid in open areas behind plants. Both species used sideways swimming movements or Leans for displacing opponents. However, C. oxyrhynchum was more aggressive, using relatively high frequencies of Tail Beating, Bite/Butting, and Tail Sweeping. They exhibited a longer latency to fight initiation, but continued to fight for longer times than C. acutirostre. Although C. oxyrhynchum were highly aggressive they did not inflict injury and this was a unifying characteristic for the three Monkengia species.

C. ansorgei the smallest and most colorful species, was not highly aggressive and in general relied on color changes and signaling displays which increased apparent size. When fights became intense they shred fins during Fin Tugging episodes. C. ansorgei and C. acutirostre shared many characteristics. Both species hid well within plant cover, swam backwards into opponents, used caudal/caudal Tail

Beating, had short bouts before resolution and used low disturbance displays. Both species are small fish, probably subject to heavy predation, and may have adapted quick resolution and low disturbance fighting as a result. *C. acutirostre* is an ambush piscivore and has a trophic strategy that also requires quick resolution and low disturbance. Both species may depend on cryptic color patterns and behavior for their well being, and agonistic repertoires have evolved to maintain and conserve these major adaptive patterns.

Thus agonistic behavior was useful to differentiate taxa on the generic level, revealing gross quantitative differences in relative frequencies of overt behaviors. However, on the lower taxonomic level, clear behavioral similarities unifying the *Monkengia* group were not detected. C. *kingsleyae* closely resembled *A. testudineus* while C. *oxyrhynchum* was most like S. *capensis* and *C. acutirostre* shared many similarities with *C. ansorgei* of the Nana group. Agonistic behavioral characteristics may have evolved along different lines reflecting strong ecological or trophic adaptations changing incidentally and not reflecting phylogeny of the group.

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