

LONGER COMMUNICATIONS

THE FIRST REPORT OF *CARCHAROCLES AURICULATUS* FROM THE OLIGOCENE OF GEORGIA IN THE CONTEXT OF PREVIOUS GULF COAST RECORDS

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ABSTRACT

Carcharocles auriculatus de Blainville, 1818 (1) is uncommon in Eocene (2) and Oligocene-aged marine vertebrate faunas of the Gulf and Atlantic coasts (3). *Carchrocles auriculatus* has been reported from the Oligocene of Mississippi (Lesueur 1828) in (3) and Florida (4), but has not been previously documented in the Oligocene of Georgia. A single tooth of *C. auriculatus* was recovered in situ from the lower Oligocene Bridgeboro Formation in Grady County, Georgia. The Bridgeboro is a calcareous algal nodule-rich limestone unit interpreted as a shallow water deposit. Primarily, *C. auriculatus* is found in littoral siliclastic or mixed siliclastic-carbonate sediments. These teeth, generally, show abrasion due to transport. Specimens collected in 'pure' carbonates may represent normal tooth loss, and have not been reworked. The dimensions (h/w ratio) from the Georgia Oligocene tooth correspond well with h/w ratios of Oligocene teeth from Mississippi and the Eocene teeth from Georgia, Mississippi, and South Carolina referred to in this study.

Key words: *Carcharocles*, sharks teeth, Eocene-Oligocene, Bridgeboro Formation

INTRODUCTION

Sharks belonging to the genus *Carcharocles* were some of the most formidable predators that ever stalked the coastal waters of Georgia. *Carcharocles auriculatus* de Blainville, 1818 (1) has also been referred to as *Carcharodon auriculatus* (5). The best-known member of the genus is the "megatooth" shark *Carcharocles megalodon*, estimated to have reached 15m in length (6). Likewise this species has been previously placed in the genus *Carcharodon*. The large teeth of this Miocene-Pliocene predator, which can reach lengths approaching 18cm (7), are highly prized by collectors and fossil dealers and are common in Atlantic Coastal

Plain deposits. A second species of this extinct laminid genus, *C. auriculatus*, has been reported from the Eocene of Georgia (8). This second species is a rather uncommon element of marine vertebrate faunas in the Twiggs Clay (Eocene). The teeth of *C. auriculatus* (Figure 1 A-D) are smaller than *C. megalodon* (Figure 1 E) and approach a maximum length around 10cm (3). The most diagnostic feature of *C. auriculatus* is the presence of large cusplets with distinctive serrations (Figure 1 A-D). Many specimens of *C. auriculatus* have been collected from the Jackson Group (Alabama, Eocene) (8). The species is less well represented in faunas from the Castle Hayne Fm. (North Carolina, Eocene), Santee Fm. (South Carolina, Eocene), Moodys Branch Fm. (Mississippi, Eocene) and Byram Fm. (Florida and Mississippi, Oligocene) (4, 3, 8).

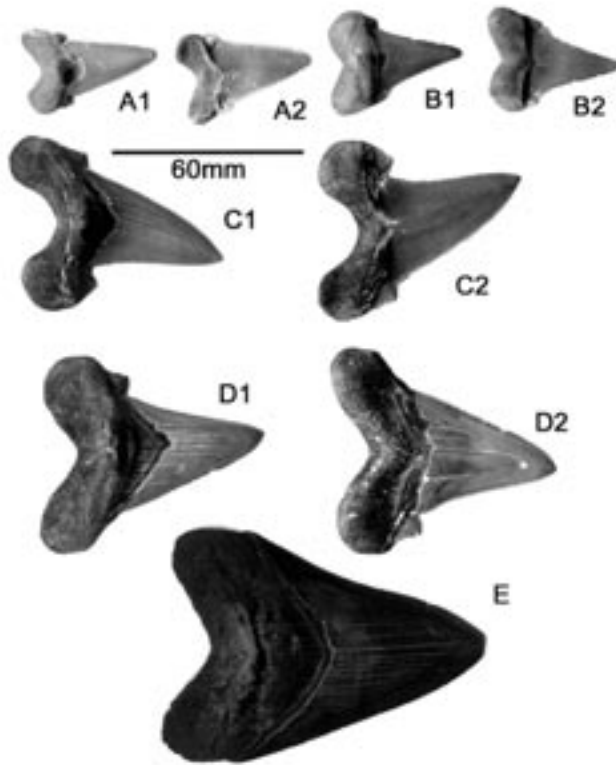


Figure 1. All teeth are to scale. One of the characters of *Carcharocles* is the presence of pronounced cusplets. Adult *C. megalodon* lacks these cusplets, but juvenile *C. megalodon* show these pronounced cusplets. Both A and B could possibly be juvenile *C. auriculatus*. **A1 & A2:** *Carcharocles auriculatus* from the Bridgeboro FM of SW Georgia showing opposing sides. **B1 & B2:** *C. auriculatus* from the Twiggs Clay, Wilkinson Co., Georgia showing opposing sides. **C1 & C2:** *C. auriculatus* from the Santee Fm., South Carolina showing opposing sides. **D1 & D2:** *C. auriculatus* from the Twiggs Clay, Wilkinson Co., Georgia showing opposing sides. **E:** *Carcharocles megalodon* showing thick robust blade and lacking lateral cusplets.

The taxonomic identities of extinct white shark species are far from resolved and there is confusion in regard to the number of species within the genus *Carcharocles*. The species *C. auriculatus* (1), *C. sokolowi* and *C. angustidens* have been described based solely on the age of the units where they were found (Middle to Late Eocene vs. Early Oligocene vs. Middle Oligocene). For the purposes of this paper, we accept Dockery and Manning's (3) treatment that the latter two are junior synonyms of *C. auriculatus*. Extinct white shark species were often placed within the extant genus *Carcharodon* with *C. carcharias* (3). For the purposes of our report, we elect to use the taxonomic delimitation advocated by Cappetta (9). Because of the following characteristics it is thought that extinct and extant white sharks are independent lineages and therefore must be placed in separate genera. The large nutritive pores of modern white sharks are distinct from the more diminutive and scattered pores present on the roots of taxa placed in *Carcharocles*. Extant white sharks tend to have upper teeth with much flatter blades than the thick, robust ones characteristic of *Carcharocles*. Systematic studies based on anatomical and molecular data (10, 11) support the viewpoint that *Isurus* and *Carcharodon* share a common ancestor. Long and Waggoner's (12) analysis, based solely on dental characters, is incongruent with the phylogenies, since the analysis suggests *Isurus* is the sister group to a clade consisting of *Carcharodon* and *Lamna*. Gottfried (13) supported placing all megatooth shark species in the genus *Carcharodon* based solely on dental characters. In our opinion, we believe that dental characters alone are not sufficient to clarify relationships within shark lineages. Treatments of modern taxa would indirectly support the viewpoint that modern white sharks have evolved independently from the giant-toothed lineages.

GEOLOGIC SETTING, MATERIALS, AND METHODS

The former Grady Aggregate Company (GAC) quarry in South Georgia is located north of Cairo, Ga in Grady County (Figure 2). The quarry was active during the past 10 to 12 years, but has been abandoned for the last two years. The tooth was collected from a small cave opening within the quarry walls. The tooth was neatly cemented within the calcarenite along with whole echinoids and the abundant calcareous nodules. The measured section at the quarry is approximately 16m. Neither the lower nor the upper contact was observed. The rock unit is the Oligocene (Vicksburgian Age) Bridgeboro Formation as described by Huddlestun (14). The type locality, as described by Manker and Carter (15), is located near the town of Bridgeboro, GA. It is a 20m thick, rhodolithic limestone in a bioclastic calcarenite matrix. Rhodoliths are nodules composed of algae belonging to division Rhodophyta (red algae). Corallinaceae or Peyssonneliaceae are the two families within the Rhodophyta that are associated with rhodolith formation. Manker and Carter (15) state that the primary algae forming the Bridgeboro rhodoliths are *Archaeolithothamnium* and *Lithoporella*. The Bridgeboro Fm. is most likely a shallow patch reef environment that has been previously described as a shelf break carbonate unit bordering the relatively deep Oligocene Suwanee Strait (15). The top of the formation at GAC contains a fine laminar encrusting algal layering as well as a decrease in rhodolith mean size. This is interpreted as a

deeper water facies (14), and possibly is laterally equivalent to the Florida Mbr. of the Bridgeboro Fm. as observed in northwestern Florida.

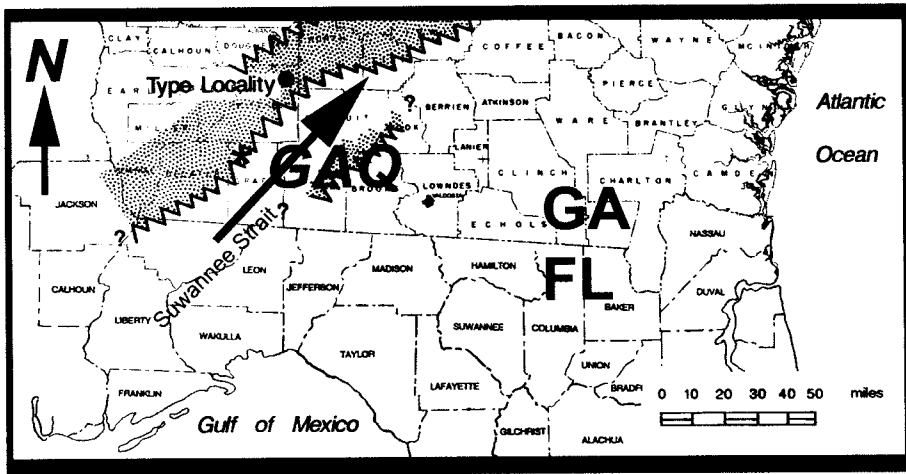


Figure 2. Location of former Grady Aggregate Company (GAC) quarry in Grady Co., GA. Map shows the Oligocene Bridgeboro Formation outcrop area (stippled pattern) and type locality section, as well as the inferred location of the Suwannee Strait. (Modified from Huddlestun (15)).

Previously in Georgia, only Eocene age specimens of *C. auriculatus* have been collected. Specimens utilized in this study for comparison with the Oligocene age tooth were collected from Riggins Mill Mbr. of the Twiggs Clay, in an inactive kaolin quarry located outside the town of Gordon, GA in Wilkinson County. Measurements were taken for the Oligocene specimen (Figure 1 A) as well as for the two Eocene specimens of *Carcharocles auriculatus* (Figure 1 B, D) recovered from the Twiggs Clay. In addition, measurements were also taken from an Eocene specimen collected from the Santee Formation of South Carolina (Figure 1 C). The overall length and width of the teeth, root and crown widths, and lengths of anterior and posterior edges were measured (Figure 3 C, Table I) at the microscopy-imaging suite in the School of Mathematical and Natural Sciences at Berry College. Dockery and Manning (3) plotted the relative height/width proportions of *Carcharocles auriculatus*. Height and width measurements from their study were combined with corresponding measurements from the present study and compared.

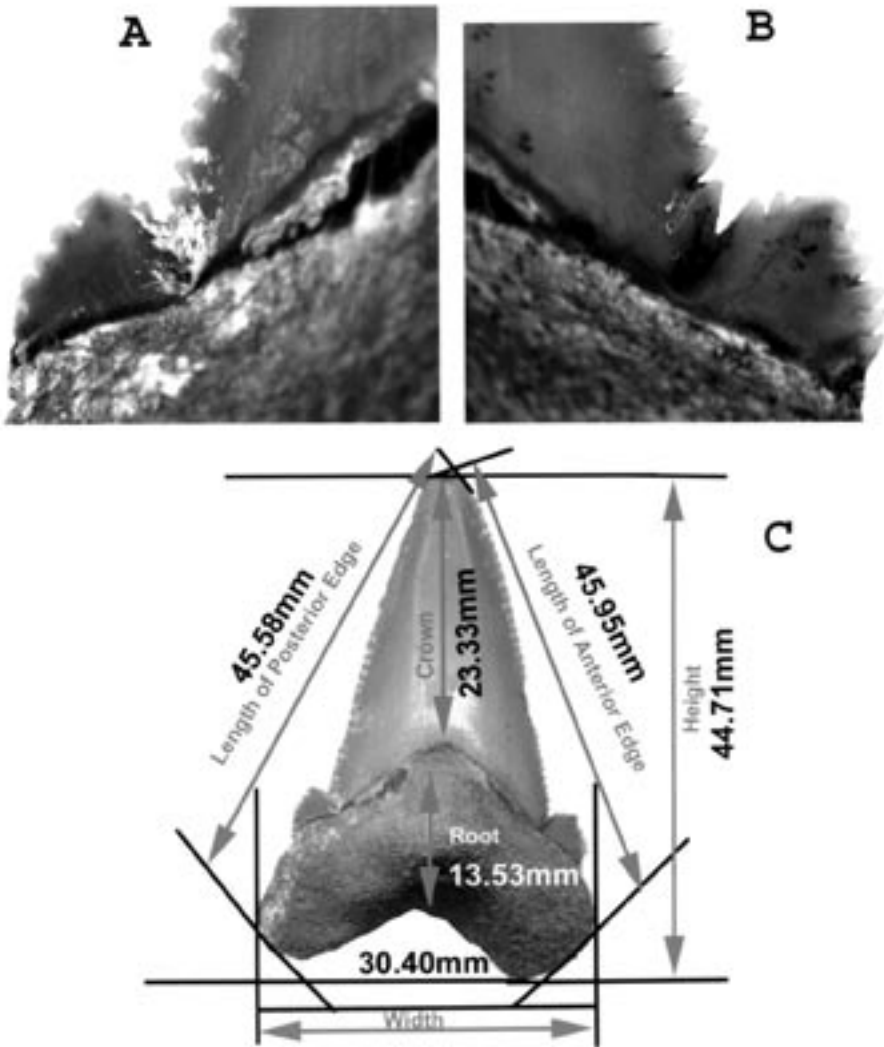


Figure 3. (A & B) Close up views of the cusplets showing well preserved and undamaged serrations (10X). (C) Diagram showing how tooth measurements were taken for this report (see Table I). Tooth specimen shown is the Oligocene Bridgeboro *Carcharocles auriculatus* specimen, which represents a first upper anterior (I) from a juvenile, in lingual view.

Table I. Linear and area measurements of some Eocene and Oligocene *Carcharocles auriculatus* teeth from Georgia (SWGA (Figure 1A), Gordon 1 (Figure 1 B) and Gordon 2 (Figure 1D) and South Carolina (SC (Figure 1 C)). Specimen data from this report are provided in the text, and all teeth from this report are featured in Figure 1. Measurements were done using a stereomicroscope utilizing a computerized imaging software program. Refer to Figure 3 for location of measurements. The dental band is the area between the root and the crown.

	SWGA	Gordon 1	Gordon 2	SC
Length in mm				
Height	44.71	44.51	76.97	75.76
Width	30.4	36.28	69.09	59.09
Root	13.53	12.94	19.39	15.46
Crown	23.33	24.52	35.45	36.36
Anterior Edge	45.95	43.48	80.66	78.28
Posterior Edge	45.58	47.5	73.86	66.68
Average Root Thickness	10.95	13.17	19.56	14.22
Area in mm²				
Crown Area	327.23	311.68	848.97	775.76
Anterior Cusplets	11.93	8.6	0	43.23
Posterior Cusplets	7.28	13.9	33.68	35.51
Root Area	367.46	475.95	1433.1	1040.89
Dental Band	33.31	41.41	217.26	104.22

RESULTS

A plot of the height and width ratio (h/w), show that the specimen collected from the Oligocene compares favorably with the other measured specimens of *Carcharocles auriculatus* reported by Dockery and Manning (3) from Mississippi (Figure 4). Measurements from the Bridgeboro specimen also compare favorably with the specimens from the Eocene of Georgia and South Carolina measured for this report (Figure 4). If we assume that all specimens are adult, then the lower teeth would be distinctly narrower than the upper teeth (3) (Figure 4). Using the graphic classification scheme proposed by Dockery and Manning (3) (as seen in Figure 4) separating lower from upper teeth, the specimen collected from the Oligocene Bridgeboro FM is an upper tooth. Because of its small size and shape it potentially represents a first upper anterior (I) tooth (17) from a juvenile. Likewise, one of the Eocene specimens from Wilkinson County may also represent an anterior tooth of a juvenile. However, the second specimen from the Wilkinson County site as well as the South Carolina specimen clearly represents upper laterals from an adult individual.

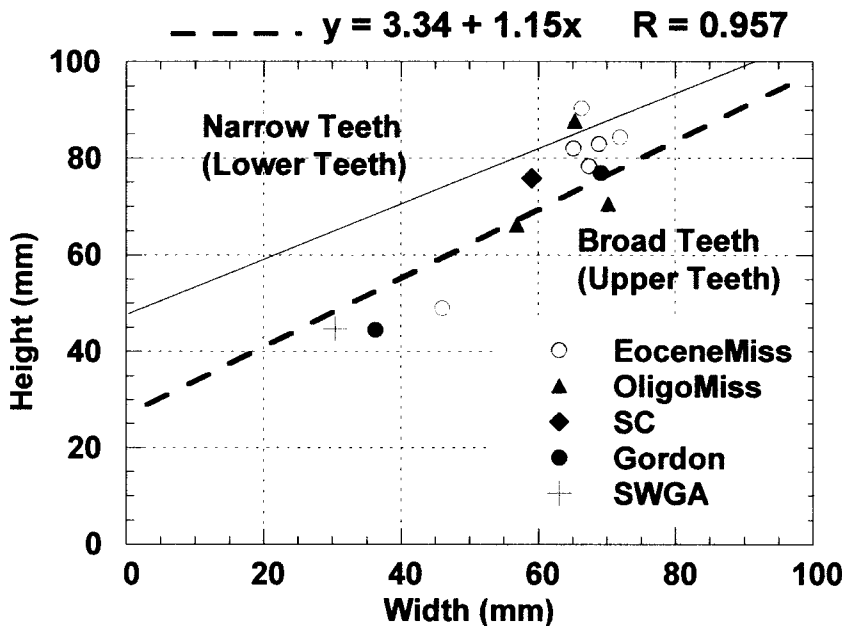


Figure 4. Graph showing relative proportion of height and width from Eocene and Oligocene specimens from Georgia (Wilkinson County site (Gordon) and Grady site (SWGA), South Carolina (SC) and Mississippi (EoceneMiss and OligoMiss). The Mississippi specimen data are from Dockery and Manning (3). The solid line represents the boundary between the narrow lower teeth and the broad upper teeth as established by Dockery and Manning (3). The dash line is the best fit linear regression ($r=0.957$) for all specimens.

DISCUSSION

The documentation of *Carcharocles auriculatus* from the Bridgeboro limestone is of particular interest. Manker and Carter (15) described 27 macrofossils from the type locality of the Bridgeboro, including some unidentified species of bryozoans, gastropods, and bivalves. These included the common echinoid *Clypeaster cotteai* and two species of scallops assigned to the genus *Chlamys*, including the common *C. duncanensis*. Another common fossil is the giant foraminifer *Lepidocyclina* sp. In the course of this study, fossils identifiable to the Order Malacostraca (spiny lobster leg segments and antennae) have also been collected from the same section of the unit where the *C. auriculatus* tooth was recovered. The biota of the Bridgeboro has been characterized as a low-diversity carbonate bank/patch reef community dominated by the red algae *Archaeolithothamnium* and *Lithoporella* (15). To date, there have been no reports of any vertebrate fossils from the Bridgeboro Formation. Furthermore, the specimen collected at the old Grady Aggregate Company quarry was not reworked from an earlier deposit. Figure 3 (A and B) nicely illustrates the excellent preservation of this tooth, note pronounced serrations of the cusplets, and the absence of abrasion damage associated with reworking. This suggests that *Carcharocles auriculatus* was a very rare, or incidental visitor to the shallow, carbonate Oligocene shoals of Georgia.

Specimens of *Carcharocles auriculatus* from the Eocene of Georgia have principally been collected from the Twiggs Clay. Purdy's (8) examinations of these specimens from the National Museum of Natural History, the Charleston Museum, and the Florida State Museum reported no teeth representing adult individuals. However, several adult teeth have been collected from the Riggins Mill Member of the Twiggs Clay Formation from the Wilkinson County site. Besides the one adult tooth collected by Parmley, reported in this paper, a private collector retrieved a second adult tooth from this site. *Carcharocles auriculatus* is a rare element of the rich elasmobranch fauna represented at the Gordon site. The material examined for this study probably represents just a fraction of the number of specimens collected at the site, which is a popular locality for amateur collectors and school groups. Based on the material at hand, and Purdy's (8) analysis of other collections of *C. auriculatus*, it is possible that the warm, shallow, coastal marginal-marine environment of the Late Eocene of central Georgia could have provided a nursery area for this species. However, at least some specimens may represent adult individuals that were washed ashore as carcasses or the occasional adult living within this marginal marine environment.

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A SURVEY OF THE MOORE CREEK FISH FAUNA, BALDWIN COUNTY, GEORGIA

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ABSTRACT

Between November 1997 and March 1998, the fish fauna of Moore Creek, Baldwin County, central Georgia was surveyed. A total of 2144 fish were collected from five habitats along a 1 km section of the stream. Represented in the fish fauna were nine families consisting of 19 species. At the family level, Cyprinidae dominated the fauna comprising 70 percent of all fish collected. Within the cyprinid family, Yellowfin Shiners (*Notropis lutipinnis*) and Bluehead Chubs (*Nocomis leptocephalus*) were the most abundant species and dominated catches from all but one habitat. The monotypic family Apredoderidae was the second most dominant family, representing 16 percent of the total fish collected. *Apredoderus sayanus* was the third most abundant species and was most common in backwater pool habitats.

Key Words: fish fauna, Moore Creek, Baldwin County, central Georgia

INTRODUCTION

While the freshwater fish fauna of the southeastern United States has been documented in some detail (e.g., 1-4), very few studies have been reported on creek or stream fish faunas of the central Georgia region. Seehorn (5) did provide some faunal survey information of the fishes occurring in southeastern national forests. More recently, Parmley and Hall (6) surveyed the fishes of Champion Creek of Baldwin County, central Georgia. Here we present the findings of a field survey of the fish fauna of Moore Creek, a typical Piedmont stream in central Georgia. The primary objectives of the survey were to document diversity aspects of the Moore Creek fish fauna.

MATERIALS AND METHODS

STUDY AREA - Moore Creek is a typical lower Piedmont clear water third order stream (Fig. 1). It originates in the lower Piedmont and terminates along the interface of the coastal plain. The selected study section of Moore Creek was a 1 km section located in Baldwin Co., central Georgia. Here the creek is characterized as a shallow, clear water creek flowing generally southeast and usually covered by a relatively dense canopy (70-75% coverage). At seasonal baseflow, Moore Creek is a series of meanders confined within well-defined banks six to eight feet high. Bedload ranged from fine silt to coarse gravel. During the survey period, water temperature averaged 52.2° Fahrenheit (range, 49-59° F) and dissolved oxygen averaged 9.3 ppm (range, 7.0-10.1 ppm). Stream width averaged 2.13 meters (range, 1.02-3.15 meters). Flow rates are reported for each habitat respectively.



Figure 1. Typical sections of Moore Creek. Depicted is a midstream run (A) and a bank run (B) habitat.

Habitats Sampled - Five habitats consistently present in Moore Creek were sampled. These included: bank runs, undercut runs, midstream runs, log pools, and backwater pools (each defined below). Two habitats are depicted in Figure 1.

Bank Run - This habitat was characterized as being a run (straight and usually at least 10 meters long) along a bank with no erosion undercutting into the bank. Water depths ranged from shallow (≤ 150 mm) to 670 mm. Mean flow was 37.50 cubic centimeters per second (ccs).

Undercut Run - This habitat was characterized as being a bank run in which water had significantly undercut the bank, adding dimension to the habitat, (i.e., protective cover, eddies, breaks in the current, and possibly diversity in food sources). This habitat ranged from shallow to about 670 mm in depth. Mean flow was 43.06 ccs.

Midstream Run - This habitat was not associated with banks or pools in any way, but rather was a central channel, usually through a bed of sand or gravel. Generally, midstream runs were shallow, ranging from 150 to 355 mm. Mean flow was relatively high at 51.86 ccs.

Log Pool - This habitat was created by water flow over a deadfall (i.e., any limb, log, or stump which water could flow over) located within a creek channel. Log pools were shallow (200 to 455 mm) and always located immediately downstream of a deadfall. Mean flow was 33.92 ccs.

Backwater Pool - This habitat was created by stream flows over deadfalls, but differed from log pools in that the deadfall was typically above the water level and positioned at or near the bank. This produced a relatively deep pool (300 to 1210 mm) distinct from channels or more centrally located and shallower log pools. This habitat was usually covered with leaf litter.

FISH SAMPLING - The study area was sampled during the winter months of November and December of 1997 and January, February and March of 1998. Ten sampling stations were established, each 30.5 meters long (midstream length) separated by a 76.0 meter stretch (midstream length) of unsampled stream. Two stations per month were operated during the sampling period with each station sampled using 20 standard minnow traps (4.2 X 19 cm, funnel opening 4-5 cm, mesh size 0.6 cm) that were open 10 consecutive days.

Minnow traps were chosen as sampling gear over more traditionally used hand dip nets and seines for the following reasons. During the study period dip nets and seines were used to sample the creek on six different occasions. Additionally, but prior to the Moore Creek study, two other central Georgia streams of similar size and physical characteristics as Moore Creek (Champion Creek and Fishing Creek) were sampled with these nets on eight occasions during summer and winter months of 1997 and 1998. In all cases, nets proved less effective than minnow traps at sampling the fish fauna. Small central Georgia streams are typically shallow and littered with rocks and/or are comprised of narrow channels making it difficult (often impossible) to utilize nets as sampling gear. It is not uncommon to encounter relatively long sections (≥ 30 m) in these creeks where the water is too shallow to effectively utilize nets, but minnow traps can be partially buried and successfully used to sample fish. In fact, four of the Moore Creek species taken by minnow traps were never taken by nets. Additionally, Parmley and Hall (6,

8) successfully used minnow traps to sample the fish fauna of Champion Creek (Baldwin Co.) when, again, nets failed to document two species and to produce the numbers of individuals that was achieved with minnow traps.

RESULTS AND DISCUSSION

A total of 2144 fishes were collected during the survey period, representing 9 families and 19 species (Table I). At the family level, Cyprinidae dominated the fauna and represent 70 percent of all fish collected. Two cyprinids, the Yellowfin Shiner (*Notropis lutipinnis*) and Bluehead Chub (*Nocomis leptocephalus*), were the most abundant species and dominated catches from all but one habitat (Table I). Aphredoderidae was the second most dominant family, representing 16 percent of the total fish collected and its single species, *Aphredoderus sayanus*, ranked third in abundance.

No specimens of larger species such as Channel catfish (*Ictalurus punctatus*), Crappie (*Pomoxis* spp.), or large individuals of the Golden Shiner (*Notemigonus crysoleucas*) were collected by nets or minnow traps. This size class may be seasonal transients with late spring and early summer high flows. Parmley and Hall (8) found that larger species in a similar sized central Georgia stream were transient with high flows and subsequent deeper water.

Habitat Accounts - For each of the Moore Creek habitats sampled, the following is given: (1) the total number of fish collected from each habitat (Table I), (2) the percent of the total number of individuals collected in that habitat (relative abundance by habitat; Fig. 2A), and (3) the percent of the total number of species collected in that habitat (species richness by habitat; Fig. 2B).

Bank Run - A total of 372 fish were collected from this habitat, comprising 17.35 percent of all fishes collected. Fourteen of the 19 species collected in total were found in this habitat (73.68 percent).

Undercut Run - A total of 781 fish were collected from this habitat, comprising 36.43 percent of all fishes collected. Seventeen species (89.47 percent of the total number of species) were found in this habitat suggesting it was the richest habitat in terms of species diversity.

Midstream Run - A total of 213 fishes were collected from this habitat (9.93 percent of all fishes collected). Fourteen species (73.68 percent of the total) were collected in this habitat.

Log Pool - Only 121 fish (5.64 percent of all fishes collected) were collected from this habitat. Additionally, only 10 species (52.63 percent of the total) were collected in the habitat.

Backwater Pool - A total of 657 fishes were collected from this habitat, comprising 30.6 percent of all the fishes collected. Fourteen species (73.7 percent of the total) were collected from this habitat.

SPECIES ACCOUNTS - Included in the following species accounts are percent abundance and percent occurrence in each habitat. Taxonomy follows Page and Burr (4) and Lee et al. (3).

Table I. Fish species collected in Moore Creek by number of individuals per habitat.

Taxon	Habitat*					Total
	BR	UR	MR	LP	BP	
Anguillidae						
<i>Anguilla rostrata</i>	1	2	1	0	5	
Esocidae						
<i>Esox americanus</i>	0	1	0	0	0	1
Cyprinidae						
<i>Hybopsis rubrifrons</i>	26	48	15	17	42	148
<i>Nocomis leptcephalus</i>	122	219	63	29	88	521
<i>Notemigonus crysoleucas</i>	0	0	1	0	0	1
<i>Notropis lutipinnis</i>	136	334	87	48	160	765
<i>Semotilus atromaculatus</i>	2	11	2	1	41	57
Catostomidae						
<i>Erimyzon oblongus</i>	0	12	0	0	6	18
<i>Moxostoma rupiscartes</i>	14	30	10	3	17	74
Ictaluridae						
<i>Ameiurus platycephalus</i>	0	3	1	2	12	18
<i>Noturus gyrinus</i>	7	19	5	2	5	38
<i>Noturus insignis</i>	4	4	1	0	1	10
Aphredoderidae						
<i>Aphredoderus sayanus</i>	37	70	13	15	203	338
Poeciliidae						
<i>Gambusia affinis</i>	0	0	0	0	4	4
Centrarchidae						
<i>Lepomis punctatus</i>	4	7	3	2	65	81
<i>Lepomis cyanellus</i>	1	1	0	0	0	2
Percidae						
<i>Etheostoma inscriptum</i>	10	9	9	2	0	30
<i>Etheostoma hopkinsi</i>	5	10	2	0	12	29
<i>Percina nigrofasciata</i>	3	1	0	0	0	4
TOTAL:	372	781	213	121	657	2144

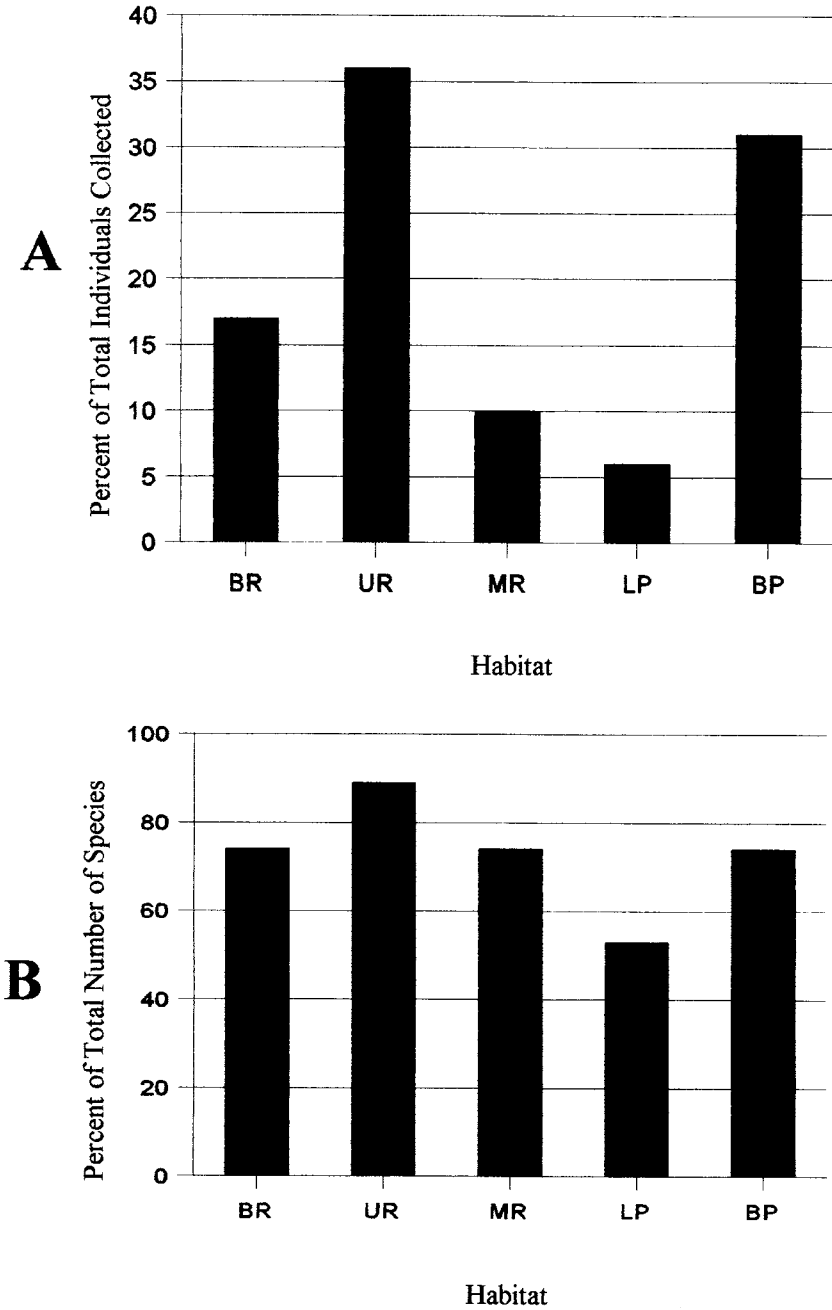


Figure 2. Fish relative abundance by habitat (A) and fish species richness by habitat (B). Abbreviations for habitats are: BR, bank run; UR, undercut run; MR, midstream run; LP, log pool; and BP, backwater pool.

ANGUILLIDAE

American Eel
(*Anguilla rostrata*)

Eels were rare, representing only 0.2 percent of all fish collected. This species was found about equally in four habitats (Table 1).

APHREDODERIDAE

Pirate Perch
(*Aphredoderus sayanus*)

Pirate perch were common in Moore Creek, comprising 16 percent of all fish collected. This species were taken in all five habitats (Table 1), but it seemed to prefer backwater pools where 60 percent of all individuals were collected.

CATOSTOMIDAE

Creek Chubsucker
(*Erimyzon oblongus*)

This species was the least common of the two catostomids sampled, and overall, was uncommon in the creek comprising only 0.8 percent of all fishes collected. The species was collected in three habitats (Table 1), although 66.7 percent of the individuals came from undercut runs.

Striped Jumrock
(*Moxostoma rupiscartes*)

The Striped Jumrock was relatively common within the survey area, comprising 3.5 percent of all fishes collected. While this species was sampled from all five habitats, it was most common in undercut runs where 40.5 percent of the individuals were collected.

CENTRARCHIDAE

Green Sunfish
(*Lepomis cyanellus*)

The Green Sunfish is not indigenous to the study area. According to Page & Burr (4), this species has been widely introduced throughout North America, which likely explains its presence in Moore Creek. *Lepomis cyanellus* was rare as only two individuals were collected (<1.0 percent of all fishes collected) from run habitats.

Spotted Sunfish
(*Lepomis punctatus*)

This species was common within the survey area, comprising 3.8 percent of all fishes collected. A strong habitat preference was suggested for the Spotted Sunfish in backwater pools as 80.2 percent were captured there.

CYPRINIDAE

Rosyface Chub
(*Hybopsis rubrifrons*)

This species was common within the survey area comprising 6.9 percent

of all fishes collected. *Hybopsis rubrifrons* were collected from all five habitats (Table 1), but were most common in undercut runs and backwater pools (32.4 and 28.4 percent respectively).

Bluehead Chub
(*Nocomis leptocephalus*)

The Bluehead Chub was common within the survey area, comprising 24.3 percent of all fishes collected. While this taxon was sampled from all five habitats (Table 1), it was most common in undercut runs (42.0 percent of all individuals collected).

Yellowfin Shiner
(*Notropis lutipinnis*)

This was the most abundant species in Moore Creek, representing 35.7 percent of all fish collected. Although the species was collected from all five habitats, it appeared to have a preference for undercut runs where 44.7 percent of all 765 individuals were captured.

Golden Shiner
(*Notemigonus crysoleucas*)

The Golden Shiner was rare within the survey area (≤ 1.0 percent of all fishes collected), with only a single individual sampled. Due to the presumed rarity of this species, percent habitat occurrence was not determined.

Creek Chub
(*Semotilus atromaculatus*)

This species was relatively common in the study area, exhibiting a 2.7 percent abundance. While *Semotilus atromaculatus* was collected from all five habitats, backwater pools appeared to be preferred by this species as 71.9 percent of all Creek Chubs sampled were from this habitat. The majority of individuals collected were juveniles. This species is typically associated with headwater streams such as Moore Creek. (4).

ESOCIDAE
Redfin Pickerel
(*Esox americanus*)

A single juvenile Redfin Pickerel was collected during the survey. This species may have been more common than is indicated here, as its reliance on eyesight in feeding (e.g., 7) may have allowed it to avoid traps.

PERCIDAE
Blackbanded Darter
(*Percina nigrofasciata*)

The Blackbanded Darter represents the only darter of the genus *Percina* collected during the study. *Percina nigrofasciata* was rare in the study area, with only four individuals collected (<1.0 percent of all fishes sampled). Consequently, habitat occurrence was not determined.

Christmas Darter
(*Etheostoma hopkinsi*)

The Christmas Darter was uncommon within the survey area (1.4 percent of all fishes sampled). The majority of individuals were taken from two characteristically different habitats: undercut runs and backwater pools (34.5 and 41.4 percent of all individuals collected respectively).

Turquoise Darter
(*Etheostoma inscriptum*)

This darter was also uncommon within the survey area (1.4 percent of all fishes sampled). The Turquoise Darter exhibited a percent occurrence which was relatively even among the three different run habitats (bank runs, 33.3 percent; undercut runs, 30.0 percent; and midstream runs, 30.0 percent).

POECILIDAE
Mosquitofish
(*Gambusia affinis*)

Mosquitofish were rare in the study area, comprising <1.0 percent of all fish collected. A total of four fish were sampled, all of which came from backwater pool habitats.

ICTALURIDAE
Flat Bullhead
(*Ameiurus platycephalus*)

Ameiurus platycephalus was rare within the study area, comprising <1.0 percent of all fishes sampled. While this fish was sampled from five habitats, percent habitat occurrence was exceptionally high from backwater pool habitats (66.7 percent).

Tadpole Madtom
(*Noturus gyrinus*)

The Tadpole Madtom was relatively common in Moore Creek (1.8 percent of all fish collected). This species was sampled from five habitats, but percent habitat occurrence was highest in undercut runs (50.0 percent). These findings are supported by Parmley & Hall (8), who found that in a central Georgia stream similar to Moore Creek in size and physical characteristics (Champion Creek) this species most commonly inhabited undercut runs.

Margined Madtom
(*Noturus insignis*)

This species was uncommon within the survey area, comprising <1.0 percent of all fishes collected. While this species was collected from four habitats, most individuals were sampled equally from bank runs and undercut runs (40.0 percent respectively).

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**BIOLOGY OF COPELATUS CAELATIPENNIS PRINCEPS YOUNG
(COLEOPTERA: DYTISCIDAE: COPELATINAE) WITH A DESCRIPTION
OF THE MATURE LARVA**

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ABSTRACT

Larvae of *Copelatus* Erichson were collected from temporary (polyxeric) woodland and roadside habitats in Jasper County, cultured into the adult stage, and identified as *C. caelatipennis princeps*. The presence of mature larvae in April was indicative of oviposition that would have occurred in mid-March. The mature larva is described and illustrated, noting the presence of four robust spines on the medial surface of the maxilla. Patterns of distribution of sensilla on the legs was similar to those previously described for mature dytiscid larvae. The number of sensilla on each leg was low (49-50) with 13 sensilla on the femur of each leg of each specimen.

Key Words: Dytiscidae; *Copelatus caelatipennis princeps*; larva; life cycle; morphology; southeastern United States.

INTRODUCTION

Copelatus Erichson includes as many as 400 species with centers of diversity in South America, Africa, and Indo-Australia (1). Only one species, *C. haemorroidalis* Fabricius is reported for Europe (2). The Nearctic fauna includes *C. blatchleyi* Young, *C. caelatipennis* Aubé, *C. chevrolati* Aubé, *C. cubaensis* Schaeffer, *C. debilis* Sharp, *C. distinctus* Aubé, *C. glyphicus* (Say), and *C. punctulatus* Aubé (3). Three subspecies are recognized within *C. caelatipennis*. *Copelatus caelatipennis angustatus* Chevrolat and *C. caelatipennis fragilis* Sharp have tropical distributions, and *C. caelatipennis princeps* Young ranges from the Bahamas into Gulf and Atlantic Coastal Plains north to New Jersey (4).

Mature larva of *Copelatus extensus* Sharp (5), *C. glyphicus* (6), and *C. parvulus* Sharp (7) have been described. De Marzo (3) provided more detailed and well-illustrated descriptions of the larval instars of *C. haemorroidalis*. Runau and Brancucci (8) evaluated a number of larval characters that they considered plesiomorphic (e.g., a well developed larval proventriculus, mandibles without channels, and cone-shaped frontoclypeal sensilla) and hypothesized that the taxon is the sister group of all other Dytiscidae. However, based on chaetotaxy of legs, Nilsson (9) postulated that larvae of Hydroporinae are more primitive than those of *C. haemorroidalis*.

The objectives of this study are to describe the mature larva of *Copelatus caelatipennis princeps*, with an emphasis on chaetotaxy of thoracic appendages, and to assess the life cycle strategy and reproductive habitat requirements of this southeastern population.

MATERIALS AND METHODS

Mature larvae of *Copelatus* were collected between 19 April and 4 May 1998 with triangular dip nets from three temporary roadside habitats (33° 14' 26"N, 83° 33' 10"W; 33° 14' 24"N, 83° 33' 27"W; 33° 13' 47"N, 83° 33' 04"W) in Jasper County, Georgia (Fig. 1A). Larvae were placed individually in petri dishes (15 by 60 mm) with moist paper towels before placement in an opaque, closed container with moist sand in the bottom (10, 11). This material was held at 18° C until adults were obtained for identification.

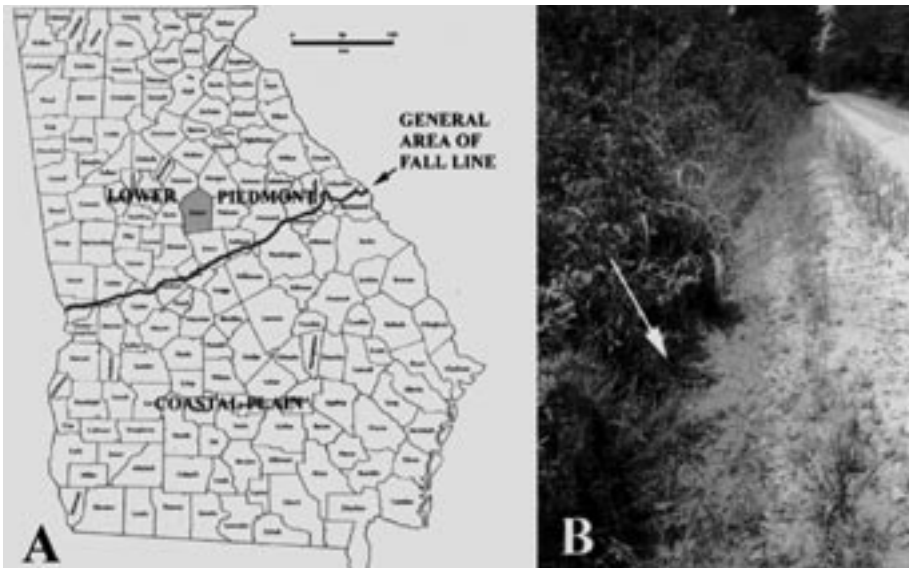


Figure 1. Georgia map indicating county collection site (A) and roadside habitat (B).

Measurements were obtained from dismembered, preserved larvae. Head lengths were measured dorsally from the posterior margin of the head to the anterior margin of the frontoclypeus along the coronal suture. Leg lengths were determined by adding the lengths of individual segments excluding trochanters. Siphon lengths were determined by subtracting the ventral length from the dorsal length of abdominal segment 8. All other measurements were taken at the longest or widest aspect. Unless noted otherwise, anatomical assessments were made from ten larvae, including two represented by cast sclerites. Common anatomical descriptive terms were used to enumerate sensilla by position or origin on segments of body and appendages. This is a modification of a system proposed by Wolfe and Roughley (12) that has proven useful for comparisons between closely related taxa (9) and evaluations of biogeographic variation (10).

RESULTS

Natural History

Mature larvae of *Copelatus* were present from 19 April through 4 May 1998 in three roadside woodland habitats where they were most frequently collected from within clumps of inundated terrestrial grasses. The habitats were temporary (polyxeric) systems (Fig. 1B) characterized by shallow water (≤ 25 cm) over clay substrates that supported few or no aquatic macrophytes. The number of larvae increased until 25 April 1998 before declining, to disappear from the habitats after 4 May. Larvae of *Hoperius planatus* Fall were present in the habitats, becoming more numerous as larval populations of *Copelatus* declined. By May, *Copelatus* larvae were infrequently collected and larvae of *Hoperius* and *Laccophilus* sp. indet. were numerous. Neither fish nor Odonate larvae were collected concurrently with *Copelatus* larvae. Hydrophilid and Chironomid larvae were collected at the sites.

Three of 12 larvae pupated on 11, 12, and 19 May. The pupal stage lasted 3-5 days ($\bar{x} = 4.3$; $n = 3$) with adults eclosing on 16, 17, and 22 May 1998.

Arthropodan appendages were present in the gut of two dismembered specimens, and a tri-lobed proventriculus (Fig. 2A) was observed in cast sclerites of three mature larvae. Acanthae of various sizes and shapes were present with the greatest variation in size on the largest lobe where relatively large placoid-like acanthae were observed.

Larval Description

General appearance.— Body cylindrical, length (alcohol preserved specimens) 5-6 mm, excluding urogomphi; sclerotized surfaces scale-like and yellowish-brown with lighter irregular areas on head and antero-medial regions of each abdominal segment.

Head.— Subquadrate in dorsal view, length 0.77-0.95 mm ($\bar{x} = 0.88$ mm), width 0.72-0.90 mm ($\bar{x} = 0.83$ mm), tapering posteriorly to form a poorly defined cervical region with prominent occipital suture; coronal suture 0.16-0.37 mm ($\bar{x} = 0.26$ mm); frontoclypeus (length 0.47-0.59 mm, $\bar{x} = 0.55$ mm) convex lateral lobes absent, anterior margin with numerous short, cone-shaped lamellae arcuate sclerotized plate attached to anterior margin below lamellae extending posteriorly into cibarium; antennal length 0.39-0.44 mm ($\bar{x} = 0.41$ mm), 1st segment 0.09-0.12

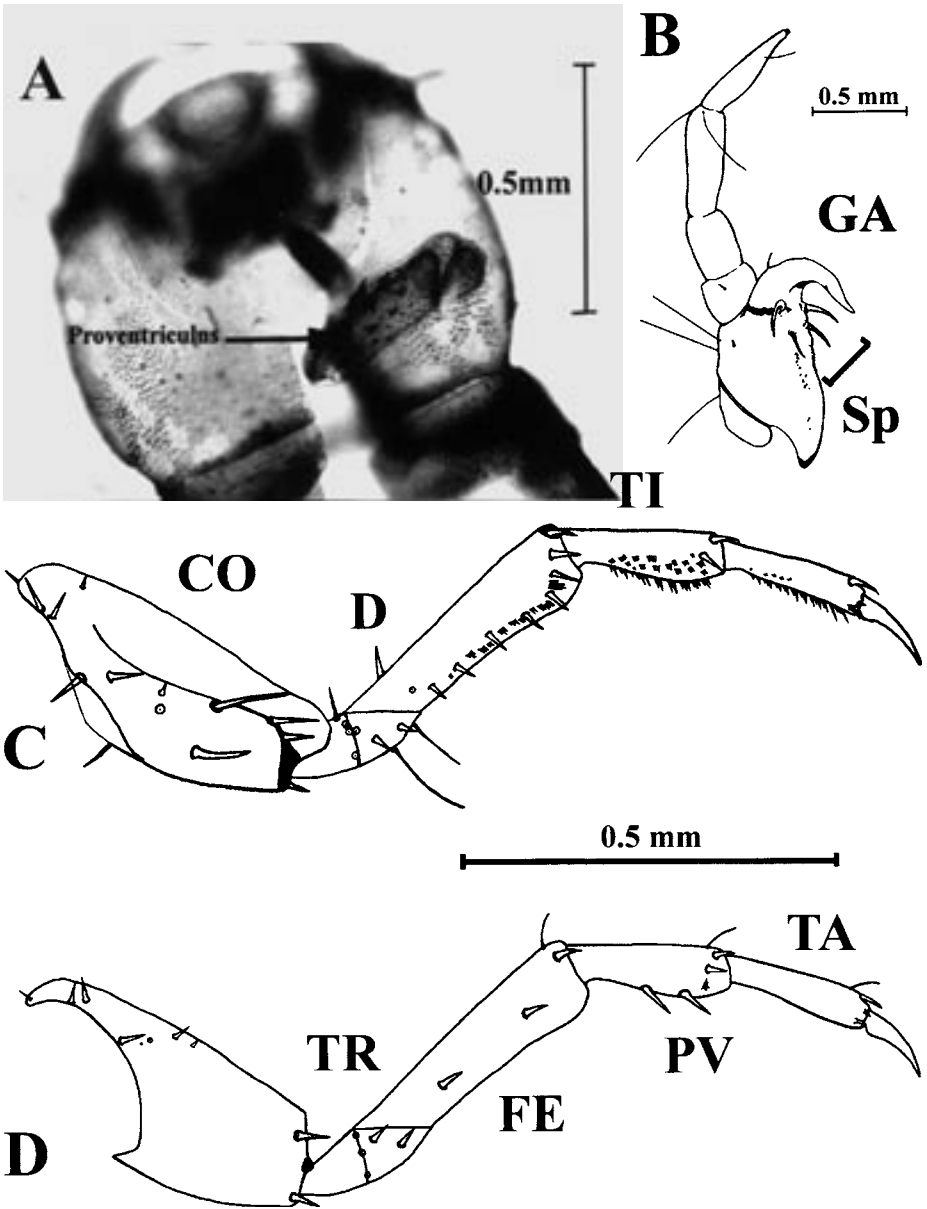


Figure 2. Proventriculus (A), maxilla (B), and anterior (C) and posterior (D) views of the proleg of *Copelatus caelatipennis princeps* Young. Abbreviations used are: CO, coxa; D, dorsal; FE, femur; GA, galea; PV, posteroventral; TA, tarsus; TI, tibia, TR, trochanters, and Sp, spur-like spines.

mm (\bar{x} = 0.10 mm), 2nd segment 0.10-0.13 mm (\bar{x} = 0.12 mm), 3rd segment 0.12-0.14 mm (\bar{x} = 0.13 mm), with three small spines and an inconspicuous accessory sensorial appendage, 4th segment 0.06-0.07 mm (\bar{x} = 0.06 mm); ocularium with one ventral, two posterior, and three antero-dorsal stemmata; gular suture obscure; posterior tentorial pits meso-ventral; sensilla of the head capsule included 3-4 temporal spines on each side and a series of long hair-like sensilla posterior to each ocularium.

Mouth parts.—Mandible falciform, mandibular channel absent, dorsal mandibular series with nine placoid-like teeth distally, ventral mandibular series with seven spine-like teeth; maxilla with one hair-like sensillum on reduced cardo, stipes with scale-like medial surface bearing two hair-like and one small sensilla ventrally, margin arcuate with four prominent spur-like spines (Fig. 2B), a small sensillum near the origin of a large claw-like galea; maxillary palp with small sensillum near origin of 1st segment (0.06-0.08 mm, \bar{x} = 0.07 mm), 2nd segment (0.09-0.12 mm, \bar{x} = 0.11 mm) with 2 distal hair-like sensilla, 3rd segment (0.11-0.13 mm, \bar{x} = 0.12 mm); with a hair-like sencillum medially; labium sub-rectangular with two small sensilla ventromedially and six peg-like spines dorsodistally, two hair-like sensilla ventrodistally near the base of each palp; labial palp with small sensillum near origin of 1st segment (0.04-0.07 mm, \bar{x} = 0.05 mm), 2nd segment (0.07-0.09 mm, \bar{x} = 0.08 mm) with prominent sensillum.

Thorax.—Pronotum trapezoidal, widest at posterior margin, bearing widely dispersed hair-like sensilla on margins and shorter sensilla widely distributed distally, two small sternites each with two minute spines; meso- and metanota subequal in length; papilliform spiracle in pleural region of mesonotum near anterolateral margin of tergite.

Legs.—(Figs. 2C & 2D). Respective lengths of pro-, meso-, and metalegs, 1.05-1.31 mm, (\bar{x} = 1.20 mm), 1.10-1.33 mm (\bar{x} = 1.20 mm), and 1.18-1.45 mm (\bar{x} = 1.30 mm), each leg of each specimen with 49-50 sensilla, without natatory sensilla; coxae with prominent anterior suture, 22-23 sensilla, each with robust anteroventral sensilla; trochanters arcuate ventrally, 7 sensilla; femora with 13 sensilla on each leg and anteroventral spinulae; tibiae and tarsi each with ventral spinulae and 7 sensilla; tarsal claw length increasing posteriorly; posterior tarsal claws about 1.1 times longer than anterior claws, each median lobe with a small sensillum.

Abdomen.—Segments 1-7 with papilliform spiracle within sclerotized tergites, hair-like sensilla arising on posterolateral margins of abdominal segment 8 becoming progressively more anterior on segments 1-7; abdominal segments 7 and 8 (0.55-0.73 mm, \bar{x} = 0.63 mm) weakly sclerotized ventrally; siphon length 0.12-0.21 mm (\bar{x} = 0.16 mm, n = 6).

Urogomphi.—Single segmented, length 0.24-0.30 mm (\bar{x} = 0.27 mm), with 4 apical sensilla, 3 sensilla arising medially, and one small spine near origin.

DISCUSSION

The habitats used for breeding by *Copelatus caelatipennis princeps* were formed by winter and early spring rains and were dry by the end of May (Fig. 1B). No information was found giving the time required for completion of the

egg and larval stages of *C. caelatipennis princeps*. However, mature larvae of some hydroporine species of comparable size that breed in temporary habitats leave the water to pupate about 30 days after adults oviposit (13). If the life cycle of *C. caelatipennis princeps* is similar to these dytiscids, the presence of mature larvae in mid-April suggests that *C. caelatipennis princeps* began oviposition in these habitats by at least mid March. This suggests that a type I (univoltine) life cycle (14) was completed at these sites by late May. However, the mild climate of the area permits dispersal of beetles throughout most of the year, and these and similar habitats are flooded again by increases in precipitation that occur typically during late summer and early fall (15). Thus, late summer and autumnal habitats are available that may be utilized as breeding sites by *C. caelatipennis princeps* and other dytiscids.

Intraspecific variation is common and the number of sensilla often increases progressively from the proleg to the metaleg on mature larvae of various dytiscid taxa (11, 16-20). However, intraspecific variation was limited to coxae of mature larvae of *Copelatus caelatipennis princeps* and the number of sensilla was the same on the remaining segments of all legs of all larvae examined. The number of sensilla on many species also increases during larval development so that mature larvae have more sensilla than either first or second instars (e.g., 21, 22). Developmental variation can only be inferred because the first instar of *C. caelatipennis princeps* is undescribed, but it will be low because the mature larva has only 13 sensilla on each femur where variation is most likely. Ten of the femoral sensilla are probable homologues of primary ancestral sensilla that are consistently present on mature larvae of most dytiscid species (9). A posteroventral sensillum on this segment is also a probable homologue of a primary sensillum present on a number of dytiscid species (23). One or both of the remaining sensilla may be homologues of additional primary sensilla, or they may be sensilla added secondarily on legs of second or third instars. In contrast, the mature larva of *C. haemorroidalis* has 16-18 profemoral sensilla (2), and the first instar has 16 (9). Thus, the mature larva of *C. caelatipennis princeps* has fewer sensilla than the larva of *C. haemorroidalis* and a more limited potential for variation.

Seven sensilla are present on the ventral surface of the stipes of *Copelatus caelatipennis princeps* (Fig. 2B). Two lateral hair-like sensilla and a smaller sensillum arising from the interior are similar to those of *C. haemorroidalis* (2) and *Colymbetinae* (24). The four remaining sensilla are massive and claw-like, dominating the medial surface below the galea (Fig. 2B). Medial spines on the stipes of *Colymbetinae* are smaller, relative to the size of the maxilla (24). Four equally prominent sensilla are present on the medial surface of the maxilla of *C. glyphicus* (6) and the Hawaiian species, *C. parvulus* (7). In contrast, the European species, *C. haemorroidalis*, has three large spines originating at this location (2, Figs. 3-7 & 3-8, SM_{1-2,3}). The differences between the sensillar patterns of the maxilla of this species and that of *C. haemorroidalis*, as well as the chaetotaxy of legs, indicate that generalities based on only a few representatives of a widely distributed genus with a large number of species should be viewed with caution.

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