To the Graduate Council:

I am submitting herewith a thesis written by Bruce L. Yeager entitled "Early Development of the Genus Carpiodes (Osteichthyes: Catostomidae)." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Zoology.

David A. Etnier, Major Professor

We have read this thesis
and recommend its acceptance

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

EARLY DEVELOPMENT OF THE GENUS CARPIODES

(OSTEICHTHYES: CATOSTOMIDAE)

A Thesis

Presented for the

Master of Science

Degree

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Bruce L. Yeager

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ABSTRACT

The early development of the three species of carpsuckers is described from the egg to the juvenile period. Means of discriminating among the carpsuckers and other suckers are described. Meristic, morphometric, morphological, and pigment pattern characters are useful for identification at the subfamily, generic, and species levels. The development of carpsuckers is similar to that of buffalos.

Among protolarval carpsuckers, hatching size, preanal myomeres, and establishment of pigment patterns are useful in taxonomic separations. For mesolarvae, metalarvae, and juveniles, head morphology and state of development at particular sizes are useful for identification of species. Of the three carpsuckers, Carpiodes velifer has consistently the smallest total length at particular stages of development. Significantly different morphometric characters are observable among the carpsuckers.

Keywords: Carpiodes carpio, Carpiodes cyprinus, Carpiodes velifer, Ictiobinae, larval development.

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INTRODUCTION

With few exceptions, life history studies of freshwater fishes in North America have omitted information on larval stages. The development, taxonomy, behavior, and ecological adaptations of larval fishes consequently are poorly understood. Recently, impetus for research on the biology of larval fishes has resulted from Federal requirements for monitoring of power plant effects on fish populations. Larval characteristics can directly affect the susceptability of particular fish species to adverse effects. Some researchers (Kramer and Smith 1962) believe that year class strength of fish is determined during the first year of life. Thus, the impingement, entrainment, passage, or pollution effects of man-made projects on young-of-the-year fishes may be of paramount importance in determining year class strength of various species.

Investigations of larval ichthyofauna have been hampered by inability to identify particular taxa of ecologically or phylogenetically related species. This report discusses aspects of the early development, taxonomy, behavior, and ecology of young of the genus Carpiodes.

The genus Carpiodes (subfamily Ictiobinae) is a member of the sucker family, Catostomidae, which is comprised of eleven North American genera (Bailey et al. 1970) and one monotypic Asian genus. A single species, Catostomus catostomus, is shared by the two continents. The three members of the genus Carpiodes are: C. carpio (Rafinesque), the river carpsucker; C. cyprinus (Lesueur), the quillback carpsucker; and C. velifer (Rafinesque), the highfin carpsucker.

Hubbs (1930) and Trautman (1957) discussed nomenclatural problems involving the species or subspecies of Carpiodes. Bailey and Allum (1962) finally synonymized the plains carpsucker, C. forbesi with the quillback carpsucker, C. cyprinus. The nomenclature utilized herein is that of Bailey et al. (1970).

The river carpsucker is distributed from Wyoming to Pennsylvania, southward along the major portion of the Mississippi River drainage and into northeastern Mexico (Moore 1957). The quillback carpsucker is distributed from southeastern Canada and the Great Lakes (except Lake Superior), west to Oklahoma, Kansas, Colorado, and Wyoming, north to Alberta, and south along the Ohio and Tennessee drainages. It occurs in the east coast drainage of North American from the St. Lawrence River to western Florida (Moore 1957, Trautman 1957, Scott and Crossman 1973). Cook (1959) lists this species from Mississippi. The highfin carpsucker occurs in the Mississippi Valley from Ohio to Mississippi, in Gulf Coast drainages to western Florida and west of the Mississippi from Nebraska to Oklahoma (Moore 1957). All three species occur sympatrically in portions of the Tennessee River drainage. In some areas of the Tennessee River Valley, the carpsuckers comprise a major portion of the catostomid population.

Fish (1932) provided limited information on larvae of five species of catostomids in Lake Erie. Fuiman (1978) described in detail the development of five species of suckers which inhabited the Atlantic Slope of North America. Winn and Miller (1954) and Fuiman (1978) provided the only attempts to formulate keys to larval suckers.

Descriptions of catostomid development of varying content have been reported on Catostomus (Crawford 1923, Stewart 1926, Macphee 1960, Weisel 1967, Long and Ballard 1976; and Fuiman 1978); Minytrema (Hogue and Buchanan 1977, White 1977); Cycleptus (Hogue 1979); Hypentelium (Buynak and Mohr 1978, Fuiman 1978); Moxostoma (Fuiman 1978, Buynak and Mohr 1979); and Erimyzon (Carnes 1958, Shaklee et al. 1974, Fuiman 1979). Information on larvae of the genus Ictiobus, the only other member of the subfamily Ictiobinae, was provided by Wrenn and Grinstead (1971) and Hoyt et al. (1979). Snyder (1979) provided information on the ranges of myomere and vertebral counts in several genera of suckers including Carpiodes and Ictiobus. Fish (1932) figured a 21 millimeter specimen of C. cyprinus, and Howarth (1961) figured a young-of-the-year C. cyprinus of unreported total length. Four original drawings of the quillback carpsucker were included in Lippson and Moran (1974). Gerlach (1973) and Fuiman (1978) provided detailed developmental studies of C. cyprinus from the northeastern United States.

May and Gasaway (1967) presented three photographs of larvae of C. carpio. No information on the development of C. velifer is available. This report provides descriptions and comparisons of the early development of the three species of carpsuckers with methods of identification and observations on behavior and ecology.

I. METHODS AND MATERIALS

Broodstock of all three species of carpsuckers was collected by electroshocking. Adult highfin carpsuckers were collected from War Eagle Creek (White River drainage) of Arkansas on May 6, 1966. Broodstock of the quillback carpsucker was obtained from the Clinch River (CRM 66.4), Tennessee on April 20, 1979. On May 2, 1979, adult river carpsuckers were obtained from the discharge channel of a steam-electric plant on the Holston River (HRM 106.2), Tennessee.

Personnel of South Central Reservoir Investigations of the United States Fish and Wildlife Service induced the highfin carpsuckers to spawn with interperitoneal injections of carp pituitary. The river and quillback carpsuckers were similarly induced to spawn. The spawning methods were those described for buffalo by Walker and Frank (1952). The eggs were incubated in McDonald jars supplied with spring water between 15 and 20 C. Larvae were cultured in phototrays (66 x 82 x 15 cm) with a continuous flow water supply. Egg yolk and finely ground trout chow were supplied to the larvae from hatching to 10 days posthatching. After 10 days, the egg yolk was discontinued and live brine shrimp (Artemis sp.) were introduced.

Specimens of highfin carpsucker were collected at varying intervals for fifty days. Young of the quillback and river carpsuckers were preserved daily in 10 percent formalin and then transferred to buffered 5 percent formalin. Series of the quillback, river, and highfin carpsuckers were catalogued as TV 1475, DS-22; TV 1476, DS-23; and TV 1477, DS-24, respectively, in the reference collection of the

Larval Fish Identification and Information Center, Tennessee Valley Authority, Norris, Tennessee.

Morphometric and meristic data were recorded utilizing a Wild M-5 stereomicroscope equipped with an ocular micrometer and polarizers. Characters examined were total length, standard length, preanal length, predorsal length, snout length, head length, head depth, body depth at the anus, eye diameter, head width, numbers of preanal and postanal myomeres, and numbers of fin rays. Morphological development and pigmentation patterns were observed and recorded.

Definitions of characters are as follows (Figure 1):

total length: the distance from the anterior tip of the snout to the posterior tip of the median finfold or candal fin, when formed.

standard length: the distance from the anterior tip of the snout to the posterior point of the urostyle.

preanal length: the distance from the anterior tip of the snout to the posterior point of the anus.

predorsal length: the distance from the anterior tip of the snout to the origin of the dorsal median finfold or dorsal fin, when formed.

head length: the distance from the anterior tip of the snout to the posterior edge of the auditory vesicle or opercle when its edge has grown posteriorly beyond the posterior edge of the auditory vesicle.

head depth: the vertical distance from the dorsum of the head to the ventrum, measured at the posterior edge of the orbit.

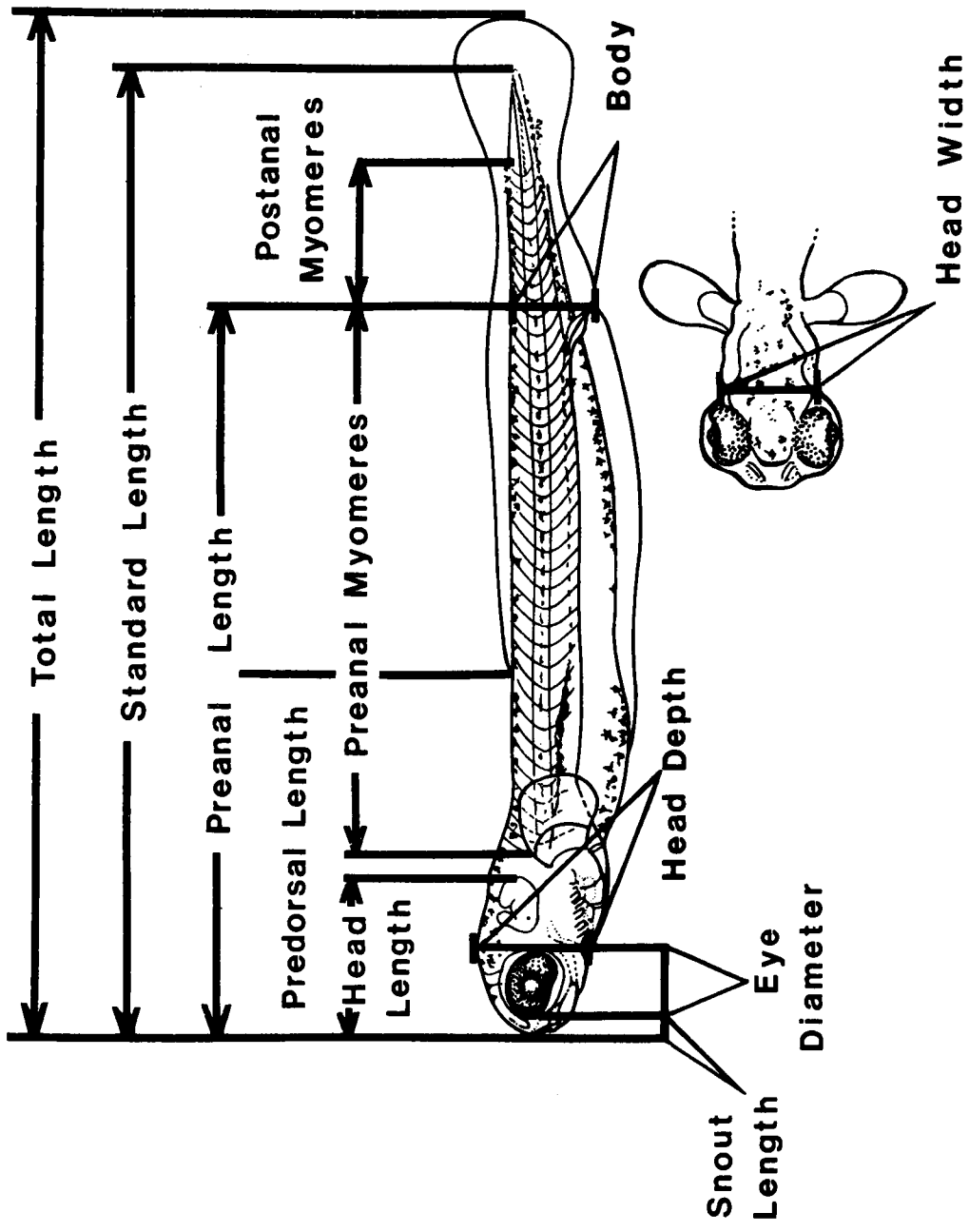


Figure 1. Methods of measurement and counting for morphometric and meristic characters examined.

body depth at the anus: the vertical distance from the dorsal edge of the body to the most ventral point of the anus, not including the median finfold.

head width: the distance from the edges, measured across the head at the posterior edge of the eyes.

Snout length and eye diameter were measured and numbers of fin rays were counted following Trautman (1957). The method of counting myomeres follows Hogue et al. (1976). Myoseptae must be complete and cross the midline for a myomere to be counted.

Drawings were made with the aid of a camera lucida. Squamation and fin ray counts were studied by staining specimens in a solution of 0.2-0.3 g/l Methylene Blue in distilled water.

The data are presented in tabular (static) form. A Statistical Analysis System (SAS) computer program was utilized for the analysis of variance. Morphometric characters mentioned in the text were significant at the $P \leq .05$ level. Broodstock of each species was obtained from single geographical areas, consequently the data from the larval series may not be applicable throughout the ranges of the three species.

Unless otherwise stated, all lengths mentioned in the text are total lengths. The terminology utilized for the descriptive material is a modified version of Snyder (1976) with reference to Hubbs (1943). Developmental periods and phases as applicable to catostomids are defined as follows:

Larval period: begins with hatching and ends with the attainment of the adult complement of rays in all fins and complete absorbtion of the median finfold.

Protolarval phase: begins at hatching when no rays are present in any fin and ends with the development of rays in any fin (the caudal fin for catostomids).

Mesolarval phase: begins with the formation of rays in any fin and ends with the attainment of the adult complement of rays in all median fins and formation of pelvic fin buds.

Metalarval phase: begins with the attainment of the adult complement of rays in all median fins, and formation of the pelvic fin buds and ends with attainment of the adult complement of rays in all fins and complete absorbtion of the median finfold.

Juvenile period: begins with the attainment of adult ray counts in all fins and complete absorbtion of the median finfold and continues until the fish reaches sexual maturity.

II. SPECIES DESCRIPTIONS

Carpiodes carpio (Rafinesque)

river carpsucker

The specimen series consisted of 244 eggs and 1,883 larvae and juveniles. Morphometric or meristic information was recorded from 270 specimens distributed as follows: 20 eggs, 48 protolarvae, 92 mesolarvae, 39 metalarvae, and 71 juveniles. Mean egg diameter was 1.8 mm and ranged from 1.7 to 2.1 mm. Specimens of cultured larvae and juveniles ranged from 5.0 to 48.2 mm.

Protolarvae

Specimens ranged from 5.0 to 11.0 mm. Means of morphometric data of protolarvae appear in Table 1. Average total length at hatching was 5.3 mm (10 specimens). Modal numbers and ranges (in parentheses) of preanal, postanal, and total myomeres of protolarvae (48 specimens) were 30 (29-31), 8-9 (6-10), and 38 (36-39), respectively.

Morphology. At hatching the head was decurved over the bulbous, club-shaped yolk sac. The yolk material was pale yellow with no oil globules. Pectoral fin buds were present and the urostyle was straight. The median finfold originated dorsally at the 10th to 12th (11th modally, 10 specimens) preanal myomere, continued around the urostyle and forward ventrally to the anterior portion of the yolk sac. The auditory vesicles were present and otoliths were visible as refracting spheres under polarized light. The oral pit was subterminal and ventral.

Table 1. Means, standard deviations and standard errors of the means for selected morphometric characters of the river carpsucker (in millimeters, ten observations per size class).

Size Range	Lengths						Depths		Eye Diameter	Head Width
	Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body		
5.02-5.53	5.30	5.11	3.87	2.16	.16	.97	.67	.40	.40	.57
S.D.	.17	.17	.18	.12	.02	.04	.03	.01	.02	.03
S.E.	.06	.05	.06	.04	.01	.01	.01	*	*	.01
6.19-6.84	6.49	6.16	4.74	2.37	.15	1.10	.78	.50	.45	.71
S.D.	.20	.20	.16	.09	.01	.04	.03	.02	.03	.04
S.E.	.06	.06	.05	.03	*	.01	.01	.01	.01	.01
7.41-7.74	7.56	7.08	5.30	2.79	.15	1.35	.80	.58	.49	.84
S.D.	.11	.12	.11	.10	.02	.03	.03	.03	.03	.01
S.E.	.03	.04	.04	.03	.01	.01	.01	.01	.01	*
8.15-8.85	8.42	7.91	5.95	3.23	.20	1.59	.93	.74	.57	.99
S.D.	.20	.19	.17	.12	.01	.03	.03	.05	.02	.03
S.E.	.06	.06	.05	.04	*	.01	.01	.01	.01	.01
9.02-9.92	9.49	8.94	6.77	3.79	.24	1.88	1.09	.86	.63	1.18
S.D.	.29	.27	.22	.22	.04	.11	.06	.04	.02	.06
S.E.	.09	.09	.07	.07	.01	.04	.02	.01	.01	.02
10.00-10.87	10.36	9.61	7.51	4.35	.32	2.13	1.23	.97	.69	1.32
S.D.	.29	.24	.25	.17	.04	.12	.08	.07	.04	.08
S.E.	.09	.08	.08	.06	.01	.04	.02	.02	.01	.03

Table 1. Continued.

Size Range	Lengths						Depths		Eye Diameter	Head Width
	Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body		
11.16-11.88	11.50	10.46	8.15	4.80	.39	2.28	1.37	1.07	.75	1.49
S.D.	.21	.18	.22	.05	.02	.09	.07	.08	.03	.06
S.E.	.07	.06	.07	.02	.01	.03	.02	.02	.01	.02
12.05-12.88	12.35	11.04	8.68	5.13	.46	2.59	1.57	1.23	.81	1.62
S.D.	.23	.16	.15	.15	.05	.12	.11	.10	.02	.06
S.E.	.07	.05	.05	.05	.02	.04	.03	.03	.01	.02
13.00-13.89	13.40	11.63	9.24	5.46	.56	2.91	1.72	1.36	.89	1.78
S.D.	.34	.24	.24	.24	.04	.17	.12	.10	.05	.09
S.E.	.11	.08	.08	.08	.01	.05	.04	.03	.02	.03
14.05-14.89	14.36	12.33	9.92	5.77	.62	3.18	1.91	1.53	.92	1.94
S.D.	.28	.31	.44	.12	.05	.15	.05	.05	.02	.05
S.E.	.09	.10	.14	.04	.02	.05	.02	.02	.01	.01
15.06-15.94	15.43	13.04	10.41	6.23	.67	3.47	2.18	1.73	1.01	2.17
S.D.	.33	.31	.31	.17	.05	.16	.11	.12	.04	.07
S.E.	.10	.10	.10	.05	.02	.05	.03	.04	.01	.02
16.06-16.81	16.35	13.57	10.64	6.40	.73	3.89	2.30	1.94	1.04	2.32
S.D.	.30	.34	.24	.18	.10	.11	.09	.08	.04	.06
S.E.	.09	.11	.08	.06	.03	.04	.03	.03	.01	.02
17.06-17.90	17.56	14.40	11.19	6.81	.75	4.16	2.54	2.24	1.13	2.53
S.D.	.23	.25	.27	.15	.10	.20	.12	.10	.06	.08
S.E.	.07	.08	.08	.05	.03	.06	.04	.03	.02	.02

Table 1. Continued.

Size Range	Lengths						Depths		Eye Diameter	Head Width
	Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body		
18.07-18.90	18.59	15.04	11.79	7.10	.75	4.39	2.70	2.53	1.20	2.65
S.D.	.23	.28	.24	.24	.07	.23	.13	.14	.05	.11
S.E.	.07	.09	.08	.08	.02	.07	.04	.04	.01	.03
19.07-19.74	19.29	15.46	12.00	7.35	.77	4.56	2.80	2.68	1.26	2.80
S.D.	.28	.28	.22	.19	.04	.10	.11	.15	.05	.09
S.E.	.09	.09	.07	.06	.01	.03	.03	.05	.02	.03
20.00-20.91	20.34	16.01	12.43	7.72	.83	4.79	2.94	2.91	1.30	2.90
S.D.	.32	.34	.36	.21	.10	.15	.08	.13	.06	.11
S.E.	.10	.11	.11	.07	.03	.05	.02	.04	.02	.03
21.08-21.92	21.46	16.67	12.74	8.08	.91	5.06	3.03	3.15	1.34	3.00
S.D.	.34	.34	.38	.21	.09	.18	.12	.10	.04	.08
S.E.	.11	.11	.12	.07	.03	.06	.04	.03	.01	.03
22.00-22.92	22.48	17.46	13.39	8.27	.95	5.32	3.24	3.31	1.39	3.17
S.D.	.28	.31	.29	.17	.06	.20	.12	.14	.06	.09
S.E.	.09	.10	.09	.05	.02	.06	.04	.05	.02	.03
23.00-23.92	23.46	18.17	13.94	8.56	.99	5.48	3.46	3.44	1.43	3.39
S.D.	.34	.34	.31	.24	.13	.28	.15	.13	.05	.14
S.E.	.11	.11	.10	.08	.04	.09	.05	.04	.01	.04

Table 1. Continued.

Size Range	Lengths						Depths		Eye Diameter	Head Width
	Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body		
24.00-24.93	24.49	18.76	14.59	8.91	1.09	5.65	3.60	3.57	1.55	3.50
S.D.	.32	.41	.46	.35	.11	.27	.18	.19	.07	.12
S.E.	.10	.13	.14	.11	.03	.09	.06	.06	.02	.04
25.10-25.93	25.55	19.76	15.28	9.59	1.19	6.04	3.78	3.76	1.54	3.68
S.D.	.33	.34	.35	.23	.06	.29	.13	.29	.06	.14
S.E.	.10	.11	.11	.07	.02	.09	.04	.09	.02	.04

* Denotes standard error of less than .01.

By 5.6 mm (one day post-hatching), the mouth was open; the head was in line with the longitudinal body axis; the eye was slightly elliptical; and the pectoral fins were paddle-like. The lower jaw grew anteriorly even with the upper jaw by 7.6 to 8.0 mm and the mouth had moved to a terminal position with the upper jaw even with the dorsal one-third of the eye.

On protolarvae about 7.7 mm (7.5 to 7.8 mm), the eye had become elliptical and was located low on the head. The snout had begun rounding down dorsally, and the ventrum of the head was flattened. The mouth was terminal but in a more ventral position than on smaller larvae. The upper jaw was level with the middle of the eye.

The opercle covered the first gill arch. The gas bladder was beginning to fill on all specimens 7.7 mm or larger. The single posterior gas bladder was ovoid with its long axis situated at a slight angle to the longitudinal body axis.

Larvae had attained a "lean" appearance with near absorption of the yolk sac. Food was already present in the gut. The yolk sac was absorbed between 7.7 and 8.2 mm, ending the prolarval phase of Hubbs (1943). Some specimens as large as 8.1 mm had retained yolk along the ventrum of the gut.

The urostyle angled up slightly between 8.4 and 9.2 mm and an opaque area formed ventral to it. The protolarval phase ended with the formation of caudal rays between 9.7 and 9.9 mm.

Pigmentation. At hatching the eyes were moderately pigmented. Yolk sac pigmentation was concentrated along the ventral midline but was

also present laterally along the yolk sac. By 6.0 mm two single postanal lines of melanophores extended ventrally from the anus to the urostyle. Between 6.7 mm and 7.5 mm (three to four days posthatching) a double dorsal row of melanophores had formed from the head to the urostyle. The pigment was continuous around the urostyle with the diffuse postanal ventral row. The dorsum of the head had ten to fifteen large melanophores and two or three large melanophores were at the posterior base of the brain. A light stitched line of melanophores was present along the entire midline. By 7.6 to 8.3 mm the dorsum of the incipient gut was pigmented and a concentration of melanophores was present at the position of the forming gas bladder tissue. Three or four large chromatophores were present over the heart region.

After yolk sac absorbtion (by 7.7-8.2 mm), a ventral diffuse line of melanophores extended from below the pectoral fins to the anus, and postanally as a diffuse row to the caudal fin. The ventral edge of the forming opercle was moderately pigmented by 8.0 to 8.7 mm. The nares each had a single crescent-shaped melanophore rimming the inside edge. By 8.5 mm the sides of the gut were pigmented and several melanophores were situated on the ventral caudal finfold, anterior to the tip of the urostyle.

Mesolarvae

Specimens ranged from 9.7 to 19.3 mm. Means of morphometric data for mesolarvae are presented in Table 1. Modal numbers and ranges of preanal, postanal, and total myomeres of mesolarvae (92 specimens) were 29 (28-31), 6 (5-9), and 35 (34-38), respectively.

Morphology. Hypural caudal rays appeared between 9.7 and 9.9 mm. The hypural complex was forming and the urostyle had angled far up by 11.6 mm. The hypural complex was complete by 13.0 mm.

In the early mesolarval phase the head became more flattened and by 10.2 mm the dorsum of the head angled down anteriorly from a point over the second gill arch. Over the posterior one-third of the eye was an indentation of the dorsal head profile that persisted into the juvenile period. The upper jaw was situated just ventral to an imaginary horizontal line even with the lower edge of the orbit by 13.6 to 15.2 mm.

Two distinct air bladders were present by 14.2 to 14.6 mm. The second air bladder initially appeared as an anterior diverticulum of the first bladder at about 12.5 mm. The posterior air bladder remained ovoid, the anterior chamber was terete.

The dorsal fin outline became apparent by 10.2 mm. The apex of the anterior portion was over the eighteenth preanal myomere. The dorsal fin was separated from the caudal finfold between 14.1 and 15.3 mm. The first dorsal fin rays formed between 12.5 and 13.4 mm, and the adult complement (24-30, mode 27) was attained between 19.1 and 19.3 mm. A few smaller specimens (17.7 to 19.1 mm) had attained ray counts (24-26) which were at the lower end of the adult range but a significant length of undifferentiated dorsal finfold remained in which one to six additional rays were present on larger specimens.

By 11.9 mm the caudal fin was slightly indented and a notch was present in the finfold dorsally where the tip of the urostyle approached the edge. The upper lobe of the caudal fin remained larger

than the lower throughout the mesolarval and metalarval phases into the early juvenile period. The adult complement of caudal rays (18) was attained between 14.2 and 14.7 mm by which size the caudal fin was distinctly emarginate.

Anal fin anlagen were visible by 14.7 mm but anal fin rays were not present until 15.6 to 16.1 mm. The anal fin was separated from the caudal finfold by 16.1 mm. The adult complement of rays was present by 17.7 to 19.4 mm.

Pectoral fin rays appeared by 13.8 to 14.2 mm. Ray development in the pectoral fin was not completed until the metalarval phase. Pelvic fin buds were apparent as tissue bulges along the ventral body wall between preanal myomeres 16 and 18 by 12.3 mm; as crescents by 12.5 mm; and as narrow based fins by 14.0 mm. Pelvic rays were present by 16.9 mm. Pelvic fin ray development was not completed in the mesolarval phase. By 17.9 mm the remaining undifferentiated finfold was confined to the preanal ventral midline.

The gut remained straight until between 12.8 and 13.4 mm when coiling began. A full gut coil was present by 13.8 to 16.1 mm. The intestine coiled to the left side of the body.

Pigmentation. The head and occiput were heavily pigmented on early mesolarvae (11.6-12.7 mm), the double dorsal row of melanophores was well defined, and the ventral edge of the opercle was outlined with melanophores. Ventrally, the heart region and foregut were lightly pigmented. The midventral area of the foregut near the origin of the ventral finfold was unpigmented. The lateral edges of the intestine were lined by a series of melanophores the entire length. Postanally,

a double row of melanophores extended from the anus to the caudal fin along the ventral midline.

The midlateral line of pigment extended to the caudal fin. The opercle directly posterior to the eye was lightly pigmented. Located on each pectoral fin base was one large melanophore. The area immediately behind the pectoral fin was heavily pigmented. The gill arches and snout were increasingly pigmented on larger specimens. Internally, the lateral sides of the brain case, the entire length of the gut dorsum, and the dorsum of the gas bladders were pigmented.

The caudal fin was pigmented to the edge by 12.7 mm. A few melanophores were sometimes present in the interradial areas of the anterior portion of the dorsal fin.

Metalarvae

Specimens ranged from 19.1 to 23.4 mm. Means of morphometric data for metalarvae are presented in Table 1 (page 10).

Morphology. Metalarvae were characterized by continued pectoral and pelvic ray development. The adult complement (8-10) of pelvic fin rays was attained between 20.9 and 22.8 mm. The last fins to attain the adult complement (15-18, mode 16) were the pectoral fins between 22.3 and 23.1 mm. All larvae attained the adult complement of rays in all fins before the complete absorbtion of the median finfold occurred. The median finfold was absorbed between 22.8 and 23.4 mm, delimiting the end of the metalarval phase.

During the metalarval phase, the single gut loop reached its farthest anterior position, almost even with the pectoral fin base. By 20.2 mm, the mouth had migrated from the central terminal position

of the early mesolarval phase to a ventral subterminal position. The characteristic dorsal depression mentioned for mesolarvae was slightly more posteriorly located, just behind the eyes.

Pigmentation. The dorsum of the head, occiput and snout were heavily pigmented on metalarvae. The number of melanophores between the two dorsal rows had increased but the double row was still observable. The dorsal and caudal fins were pigmented to the edge, and the anal fin about half way to the edge. Dorsolateral pigmentation increased, but below the midline pigmentation was sparse. Ventrally, a double row of melanophores extended around the anal fin and thereafter was a diffuse single row to the caudal fin base. Internally, the foregut pigment was heavier than on mesolarvae.

Juveniles

Specimens ranged from 22.8 to 48.2 mm. Means of morphometric data for juveniles are presented in Table 1 (page 10). Ranges and modes of fin ray counts for juveniles are given in Table 2.

Morphology. The mouths of juveniles remained inferior and subterminal with fleshy lips. The posterior edge of the lips, when viewed laterally, was even with or posterior to the anterior edge of the orbit. The characteristic head indentation over the eye, noted for mesolarvae and metalarvae was retained in the early juvenile period. The head had become more fusiform and not so flattened ventrally.

Table 2. Modal numbers and ranges of fin rays of early juvenile carpsuckers. Mode (range)

Species	Number of Specimens	Dorsal Fin Rays	Anal Fin Rays	Caudal Fin Rays	Pectoral Fin Rays	Pelvic Fin Rays
Carpiodes carpio river carpsucker	40	27 (24-30)	8 (7-9)	18 (17-19)	16 (15-18)	9 (8-10)
Carpiodes cyprinus quillback carpsucker	40	29 (25-30)	8 (7-8)	18 (16-18)	16 (16-18)	10 (9-10)
Carpiodes velifer highfin carpsucker	4	25 (25-27)	8 (8-9)	18 (17-19)	16 (16-17)	10 (10-11)

Squamation was first observed as placodes forming on the lower caudal peduncle at 20.3 mm. Scale formation occurred posteriorly to anteriorly. The last areas to form scales were the nape and the breast. Squamation was completed by 31.8 to 34.0 mm.

Pigmentation. Overall pigmentation increased over that of metalarvae. The lower jaw was heavily pigmented. The pelvic and pectoral fins remained unpigmented on the largest specimen examined (48.2 mm).

Carpiodes cyprinus (LeSueur)

quillback carpsucker

The specimen series consists of 10 eggs and 2,591 larvae and juveniles. Meristic and morphometric data were recorded from 251 specimens distributed as follows: 10 eggs, 41 protolarvae, 98 mesolarvae, 47 metalarvae, and 55 juveniles. Mean egg diameter was 2.1 mm (10 specimens) and ranged from 2.0 to 2.2 mm. Specimens of cultured larvae and juveniles ranged from 5.8 to 57.4 mm.

Protolarvae

Specimens ranged from 5.8 to 11.0 mm. Means of morphometric data for protolarvae appear in Table 3. Average size at hatching was 6.5 mm (14 specimens). Modal numbers and ranges of preanal, postanal, and total myomeres for protolarvae (41 specimens) were 31 (29-32), 9 (7-11), and 40 (37-42), respectively.

Morphology. The heads of newly hatched larvae were strongly decurved over the yolk sac. The yolk sac was elongate and club shaped.

Table 3. Means, standard deviations and standard errors of the means for selected morphometric characters of the quillback carpsucker (in millimeters, all size intervals except five millimeter class have ten observations).

Size Range	Lengths						Depths		Eye Diameter	Head Width
	Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body		
5.72+	5.72	5.52	4.49	2.77	.18	1.07	.71	.46	.47	.56
6.26-6.96	6.62	6.35	4.85	2.60	.18	1.10	.81	.55	.46	.69
S.D.	.26	.24	.16	.11	.02	.06	.06	.03	.02	.06
S.E.	.08	.08	.05	.03	.01	.02	.02	.01	*	.02
7.08-7.91	7.44	7.12	5.35	2.61	.18	1.19	.84	.60	.50	.79
S.D.	.27	.24	.22	.13	.01	.04	.02	.02	.02	.06
S.E.	.08	.08	.07	.04	*	.01	.01	.01	.01	.02
8.03-8.98	8.52	8.04	6.08	3.05	.17	1.34	.92	.64	.53	.86
S.D.	.30	.29	.17	.14	.02	.03	.05	.03	.02	.03
S.E.	.09	.09	.05	.04	.01	.01	.02	.01	.01	.01
9.06-9.88	9.54	8.98	6.68	3.40	.20	1.62	1.00	.73	.61	.99
S.D.	.31	.32	.24	.20	.02	.05	.03	.04	.01	.03
S.E.	.10	.10	.08	.06	.01	.02	.01	.01	*	.01
10.05-10.87	10.38	9.81	7.27	3.72	.24	1.87	1.07	.79	.65	1.08
S.D.	.28	.28	.19	.14	.02	.05	.05	.05	.03	.04
S.E.	.09	.09	.06	.04	.01	.02	.02	.01	.01	.01

Table 3. Continued.

Size Range	Lengths						Depths		Eye Diameter	Head Width
	Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body		
11.06-11.89	11.42	10.75	8.09	4.53	.38	2.35	1.28	.98	.79	1.34
S.D.	.30	.27	.26	.27	.04	.12	.06	.08	.04	.09
S.E.	.09	.08	.08	.09	.01	.04	.02	.03	.01	.03
12.14-12.56	12.39	11.54	8.81	4.95	.42	2.48	1.43	1.10	.84	1.46
S.D.	.14	.15	.11	.12	.03	.43	.07	.05	.03	.07
S.E.	.05	.05	.04	.04	.01	.14	.02	.02	.01	.021
13.15-13.90	13.43	12.26	9.34	5.10	.46	2.76	1.59	1.17	.90	1.65
S.D.	.20	.23	.23	.19	.03	.06	.05	.06	.03	.04
S.E.	.06	.07	.07	.06	.01	.02	.02	.02	.01	.01
14.07-14.91	14.54	12.62	9.85	5.65	.57	3.07	1.82	1.34	1.00	1.86
S.D.	.31	.28	.25	.14	.05	.17	.08	.06	.03	.07
S.E.	.10	.09	.08	.05	.02	.05	.02	.02	.01	.02
15.08-15.75	15.41	13.18	10.48	5.94	.60	3.28	2.03	1.54	1.08	2.01
S.D.	.26	.21	.31	.13	.05	.12	.07	.13	.04	.05
S.E.	.08	.07	.10	.04	.02	.04	.02	.04	.01	.02
16.05-16.83	16.43	13.67	10.71	6.13	.64	3.49	2.27	1.70	1.13	2.19
S.D.	.25	.29	.28	.23	.07	.22	.08	.07	.05	.06
S.E.	.08	.09	.09	.07	.02	.07	.03	.02	.01	.02
17.00-17.92	17.46	14.57	11.59	6.46	.71	3.81	2.39	1.83	1.19	2.37
S.D.	.35	.30	.26	.16	.06	.19	.10	.10	.05	.11
S.E.	.11	.10	.08	.05	.02	.06	.03	.03	.02	.04

Table 3. Continued.

Size Range	Lengths						Depths		Eye Diameter	Head Width
	Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body		
18.17-18.68	18.40	15.03	11.95	6.86	.82	4.11	2.60	2.00	1.25	2.54
S.D.	.19	.15	.12	.24	.08	.19	.13	.15	.05	.14
S.E.	.06	.05	.04	.08	.03	.06	.04	.05	.02	.04
19.10-19.93	19.43	15.70	12.28	7.21	.81	4.42	2.90	2.40	1.34	2.73
S.D.	.29	.29	.36	.26	.07	.17	.11	.12	.04	.09
S.E.	.09	.09	.11	.08	.02	.05	.04	.04	.01	.03
20.02-20.77	20.35	16.53	13.02	7.60	.91	4.60	3.05	2.54	1.35	2.85
S.D.	.28	.21	.33	.24	.10	.17	.09	.13	.04	.11
S.E.	.09	.06	.11	.07	.03	.05	.03	.04	.01	.03
21.11-21.78	21.46	16.88	12.78	7.99	.80	4.97	3.27	2.85	1.45	3.03
S.D.	.20	.44	.25	.19	.09	.22	.12	.10	.09	.13
S.E.	.06	.14	.08	.06	.03	.07	.04	.03	.03	.04
22.11-22.78	22.40	17.12	13.01	8.13	.85	5.26	3.47	2.99	1.57	3.17
S.D.	.24	.31	.17	.22	.12	.19	.16	.18	.05	.12
S.E.	.08	.10	.05	.07	.04	.06	.05	.06	.02	.04
23.03-23.87	23.46	18.00	13.69	8.67	.89	5.51	3.69	3.25	1.61	3.21
S.D.	.30	.23	.24	.17	.11	.23	.18	.15	.06	.09
S.E.	.10	.07	.08	.05	.03	.07	.06	.05	.02	.03
24.12-24.79	24.36	18.41	14.04	8.82	1.02	5.76	3.87	3.52	1.68	3.41
S.D.	.21	.21	.11	.29	.09	.22	.16	.16	.05	.18
S.E.	.07	.07	.04	.09	.03	.07	.05	.05	.02	.06

Table 3. Continued.

Size Range	Lengths						Depths		Eye Diameter	Head Width
	Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body		
25.13-25.96	25.60	19.36	14.85	9.15	1.13	6.08	4.07	3.75	1.73	3.60
S.D.	.29	.45	.43	.31	.15	.45	.20	.17	.04	.12
S.E.	.09	.14	.14	.10	.05	.14	.06	.05	.01	.04

+ Denotes a single observation in this length category

* Denotes standard error of less than .01

The urostyle was straight. The oral groove was present but the mouth was not open. Auditory vesicles and otoliths were present. Incipient gill arches were observed as tissue folds. The median finfold originated dorsally at the 10th to 12th preanal myomere (11th modally, 10 specimens) and continued around the urostyle forward ventrally to the anterior one-third of the yolk sac. It extended anteriorly to the anterior one-third of the yolk sac. Pectoral fin buds were present at hatching.

By two days posthatching (7.2-7.9 mm), the head was in line with the longitudinal body axis and the mouth was open. The yolk sac was more tubular. The eye was becoming elliptical and was definitely so by 8.1 to 8.7 mm. The gill arches were well formed with gill rakers forming as blunt knobs on the arches by 8.1 to 8.3 mm. The pectoral fins were paddlelike.

The mouth remained subterminal until 8.8 mm when it became terminal. The lower jaw did not grow out even with or beyond the upper jaw until about 9.7 mm. By this total length, the lower jaw was at a distinctly oblique angle.

Between 8.6 and 9.2 mm the gas bladder began to fill. Throughout the remaining protolarval phase, the single gas bladder remained ovoid. The head became slender and distinctly flattened ventrally.

At eight days posthatching (9.1-9.6 mm), the yolk sac was absorbed. The apex of the forming dorsal fin was apparent over the 16th or 17th preanal myomere on late protolarvae. During the late protolarval phase (9.9-11.0 mm), an opaque area formed ventral to the

urostyle, precursing caudal ray development. The hypural complex and basal supports for fin rays were also present. The protolarval phase ended with the formation of caudal rays between 10.0 and 11.0 mm.

Pigmentation. At hatching, the yolk sac was moderately to heavily pigmented both ventrally and laterally. The eye was pigmented and a diffuse line of melanophores extended from the anus to the caudal fin. Internally, several large chromatophores were present along the length of the dorsum of the notochord and persisted into the mesolarval phase.

By 7.1 mm (two days posthatching), the yolk sac pigment had intensified along the ventral midline. The dorsum of the heart region and yolk sac was darkly pigmented. Five or six melanophores were present along the dorsum at this size but the distinct double dorsal row of melanophores was not present until three to four days posthatching (7.9-8.1 mm). By this time the head and occiput were covered with about 30 melanophores; the base of the brain was pigmented; the dorsum of the yolk sac was heavily pigmented along the incipient gut; and the dorsal and postanal ventral pigment was continuous around the urostyle. A midlateral line of melanophores from over the incipient gas bladder to the caudal fin base was present by 8.6 mm. The otoliths were pigmented with three or four large chromatophores in each auditory vesicle. On specimens 9.9 mm or larger the caudal finfold had several chromatophores in the "streaked" region where incipient rays were forming.

On late protolarvae (10.2-11.0 mm), heavy pigment on the base of the brain connected internally with pigment along the dorsum

of the gut. A diffuse lateral line of melanophores along the gut fused anteriorly with the heavy ventral pigment of the heart and foregut region. The dorsum of the heart and auditory vesicles was heavily pigmented. The upper jaw was outlined with melanophores and the snout had 10 to 12 melanophores. The ventral edge of the opercle was stitched with melanophores and five or six chromatophores were present laterally. The gill arches were lined with melanophores.

Mesolarvae

The total length range of mesolarval specimens examined was 10.0-20.6 mm. Means of morphometric data are presented in Table 3. Modal numbers and ranges of preanal, postanal, and total myomeres for mesolarvae (98 specimens) were 29-30 (28-32), 6 (5-11), and 35 (34-42), respectively.

Morphology. The appearance of caudal rays between 10.0 and 11.0 mm marked the beginning of the mesolarval phase. The caudal finfold became truncated by 11.7 to 12.4 mm. The posterior margin of the caudal fin again rounded out as more caudal rays were formed (12.9 mm). The notch in the caudal fin margin near the tip of the urostyle was present. The caudal fin was indented by 13.2 to 15.6 mm and deeply emarginate by 16.4 mm. By 15.5 mm, the adult complement of caudal fin rays (18) was present and development of the hypural complex was complete.

Anterior dorsal rays appeared between 14.2 and 15.1 mm. The dorsal, caudal, and anal finfolds were continuous until 17.1 mm. The dorsal fin attained the adult complement (25-30, modally 29) of fin rays between 19.7 and 20.6 mm.

Between 12.0 and 12.7 mm the pelvic fin buds appeared as tissue bulges along the exterior ventral gut wall and by 13.0 mm were wide-based flaps. Pelvic rays appeared by 17.6 to 19.2 mm. The pelvic fins did not grow beyond the edge of the median finfold, when viewed laterally, until 18.4 mm. Anal rays appeared by 16.4 to 16.9 mm; the adult complement (7-8, 8 modally) was present by 19.7 to 20.6 mm. By 16.4 to 17.1 mm three or four pectoral rays were present. Pectoral and pelvic fin ray development was not completed in the mesolarval phase.

The single ovoid gas bladder began to branch off anteriorly by 12.0 to 13.4 mm. Two distinct gas bladders were present by 14.4 mm.

By 16.6 mm the upper jaw had migrated ventrally to a point well below the lower edge of the eye on all specimens. The head remained flattened throughout the mesolarval phase. The dorsum of the head rounded down smoothly from the occiput to the tip of the snout.

The range of sizes for the appearance of a full gut coil coincided with the range for the first observable bending of the gut (16.4-17.1 mm). The intestine coiled to the left side of the body.

Pigmentation. Early mesolarval pigmentation was the same as that described for late protolarvae. By 12.0 mm the gular region had many small melanophores. A stitched line of small melanophores rimmed the orbit. From the heavily pigmented dorsum of the heart region, a line of melanophores extended posteriorly over the gas bladder and dorsum of the gut to the anus. Another line of melanophores extended along the lateral sides of the gut. A third

row extended the length of the intestine ventrum. The midlateral line of pigment continued onto the opercle to a concentration of melanophores just behind the eye. The opercle was heavily pigmented by 14.1 mm. Ventrally, mesolarvae lacked pigment near the origin of the finfold.

By 15.5 mm the dorsolateral area was moderately pigmented, the nares were outlined, and the pectoral fin supports were pigmented. Several melanophores were present on the cheeks by 16.4 mm. Dorsolateral pigmentation increased throughout the mesolarval phase.

The caudal fin rays were "stitched" to the edge by 13.0 mm. The anterior dorsal fin was pigmented in the inter-radial areas by 14.2 mm, and along the entire length by 19.9 mm. The anal and pectoral fins had several melanophores in the proximal portions by 16.7 mm.

Metalarvae

Specimens of metalarval quillback carpsuckers examined ranged from 19.7 to 25.6 mm. Means of morphometric data are presented in Table 3 (page 22).

Morphology. The adult complements of median fin rays were attained between 19.7 and 20.6 mm. The pelvic fins attained the adult complement of rays (9-10) between 21.6 and 22.3 mm. The adult complement of pectoral fin rays (15-18) was attained between 22.8 and 23.9 mm. The median finfold was absorbed between 24.8 and 25.6 mm, delimiting the end of the metalarval phase.

During the metalarval phase the first gut loop did not extend to the anterior foregut as in the river carpsucker. The head retained the smoothly sloped curvature from the occiput to the tip of the snout.

The mouth had already migrated to a ventral subterminal position by 18.8 mm.

Pigmentation. Dorsal pigmentation from the snout to the base of the caudal fin was heavy. Many smaller chromatophores had developed between the two dorsal rows of larger chromatophores. A mid-dorsal concentration of melanophores was present posteriorly to the origin of the dorsal fin.

An irregular double row of melanophores was present along the ventrum of the gut and anal fin. A diffuse row of melanophores was present postanally to the caudal fin base. The ventral edge of the opercle, gill arches, snout, and upper jaw were heavily pigmented. The opercle had many large melanophores. The ventral and posterior portions of the orbit were stitched with small melanophores. Below the midline moderate pigment was present posteriorly to the pelvic fins. Posterior to the pelvic fins ventrolateral pigmentation was heavy. Pigmentation along the dorsolateral area was heavy. Internally, the gas bladder and gut were heavily pigmented. The anal, dorsal, and caudal fins were pigmented to the edge. The pelvic and pectoral fins were unpigmented.

Juveniles

Juvenile quillback carpsuckers examined ranged between 24.8 and 57.4 mm. Ranges and modal numbers of fin rays of juveniles are given in Table 2 (page 20). Means of morphometric data for juveniles are shown in Table 3 (page 22).

Morphology. Mouths of juveniles remained ventral and subterminal. When viewed laterally, the posterior edge of the mouth

was anterior to the front edge of the orbit. The head of the juvenile quillback carpsucker lacked the depressions of the other two species of carpsucker, and was of a "blockier" appearance. The pelvic fins were located slightly more posteriorly on the quillback than on the other carpsuckers.

Squamation was similar to that of the river carpsucker. Formation of scales began as placodes on the caudal peduncle by 19.8 to 20.9 mm and proceeded anteriorly, reaching the cleithrum by 23.8 mm. By 30.1 mm, the entire body was scaled except for the breast and belly. Squamation was completed by 37.0 mm.

Pigmentation. Early juvenile pigmentation resembled metalarval pigmentation patterns. Juveniles were heavily pigmented laterally. Between 22.8 and 34.3 seven to nine longitudinal body stripes developed. The middle three stripes were the darkest. The ventrum from the isthmus to the origin of the anal fin was sparsely pigmented. The gular region and branchiostegals were moderately pigmented. A concentration of melanophores was present on the posterior edge of the gill aperture. Scales were outlined on the posterior edges. The dorsal, anal, caudal, and pectoral fins were pigmented to the edges on larger specimens (25.0-34.3 mm). The middle five rays of the pelvic fins were lightly pigmented.

Carpiodes velifer (Rafinesque)

highfin carpsucker

The series of highfin carpsuckers consists of 412 eggs and 188 larvae and juveniles. Morphometric and meristic data were recorded

from 115 specimens, distributed as follows: 32 eggs, 35 protolarvae, 41 mesolarvae, 3 metalarvae, and 4 juveniles. Mean egg diameter was 2.0 mm and ranged from 1.9 to 2.0 mm. Specimens of cultured young ranged from 5.4 to 36.2 mm.

Protolarvae

Specimens ranged from 5.4 to 9.1 mm. Means of morphometric data for protolarvae appear in Table 4. Larvae were not preserved at hatching, but one-day-old larvae averaged 5.6 mm (five specimens). Modal numbers and ranges of preanal, postanal, and total myomeres for protolarvae (35 specimens) were 29 (26-29), 8 (6-10), and 37 (35-39), respectively.

Morphology. The head was only slightly decurved over the yolk sac at one-day posthatching (5.6 mm). The yolk sac was club shaped. The mouth was open but distinctly subterminal and ventral. Auditory vesicles were visible under polarized light. Incipient gill arches were present as tissue folds. Pectoral fin buds were present and the urostyle was straight. The median finfold originated dorsally at the 10th or 11th preanal myomere (11th modally) and was continuous around the urostyle forward ventrally to the anus. The ventral finfold extended forward to the anterior one-third of the yolk sac.

By 6.0 mm the head was in line with the body axis, pectoral fins were paddlelike, and the eye was becoming elliptical. By 6.9 mm the mouth was terminal, the dorsal edge of the upper jaw was situated even with the middle of the orbit, and the lower jaw as at an oblique angle. Four or five gill rakers were apparent on each arch by 6.9 mm.

Table 4. Means, standard deviations and standard errors of the means for selected morphometric characters of the highfin carpsucker (in millimeters).

Size Range	Number of Specimens	Lengths						Depths			
		Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body	Eye Diameter	Head Width
5.44-5.85	5	5.65	5.38	4.04	2.21+	.19+	1.03+	.69+	.46	.24+	.58
S.D.		.17	.15	.10					.05		
S.E.		.08	.07	.04					.02		
6.01-6.92	10	6.65	6.29	4.75	2.48	.12	1.12	.75	.56	.48	.71
S.D.		.34	.31	.26	.13	.02	.06	.04	.02	.04	.03
S.E.		.11	.10	.08	.04	.01	.02	.01	.01	.01	.01
7.04-7.74	10	7.51	7.05	5.27	2.80	.16	1.35	.83	.61	.50	.85
S.D.		.20	.18	.15	.15	.03	.08	.03	.02	.02	.06
S.E.		.06	.06	.05	.05	.01	.02	.01	.01	.01	.02
8.07-8.81	10	8.55	8.06	6.05	3.29	.27	1.68	.88	.68	.60	.99
S.D.		.22	.25	.17	.10	.04	.05	.06	.04	.01	.04
S.E.		.07	.08	.05	.03	.01	.02	.02	.01	*	.01
9.06-9.72	10	9.26	8.71	6.58	3.63	.31	1.88	.96	.78	.65	1.10
S.E.		.21	.22	.20	.17	.04	.10	.04	.04	.04	.05
S.D.		.07	.07	.06	.05	.01	.03	.03	.01	.01	.01
10.05-10.97	10	10.48	9.66	7.38	4.36	.46	2.22	1.22	.94	.70	1.34
S.D.		.34	.29	.29	.10	.03	.11	.08	.07	.05	.06
S.E.		.11	.09	.09	.03	.01	.03	.03	.02	.02	.02

Table 4. Continued.

Size Range	Number of Specimens	Lengths						Depths			
		Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body	Eye Diameter	Head Width
11.06-11.81	10	11.38	10.02	7.82	4.78	.52	2.44	1.32	1.04	.77	1.53
S.D.		.32	.20	.24	.23	.02	.08	.07	.05	.02	.05
S.E.		.10	.06	.08	.07	.01	.03	.02	.01	.01	.01
12.23-12.73	3	12.42	10.92	8.41	5.25	.58	2.74	1.52	1.22	.84	1.77
S.D.		.27	.56	.21	.17	.03	.20	.09	.13	.01	.09
S.E.		.16	.32	.12	.10	.02	.11	.05	.08	.01	.05
13.15-13.40	2	13.28	11.06+	9.09	5.31	.59	3.17	1.54	1.36	.86	1.83
S.D.		.18		.06	.06	.04	.06	.07	.04	.04	.04
S.E.		.13		.04	.04	.03	.04	.05	.03	.03	.03
14.07-14.49	3	14.32	11.78	9.50	5.74	.68	3.49	1.82	1.50	.91	1.99
S.D.		.22	.19	.14	.10	.04	.11	.03	.11	.04	.03
S.E.		.13	.11	.08	.06	.02	.06	.01	.06	.02	.02
15.08-15.75	2	15.42	12.48	9.89	6.14	.70	3.64	2.03	1.84	1.02	2.22
S.D.		.47	.35	.47	.06	.07	.03	.04	.06	.10	.06
S.E.		.34	.25	.34	.05	.05	.02	.03	.05	.07	.04
16.25-16.58	3	16.39	12.90	10.19	6.45	.69	4.16	2.39	2.12	1.12	2.39
S.D.		.17	.17	.26	.13	.09	.15	.12	.09	.06	.04
S.E.		.10	.10	.15	.07	.05	.09	.07	.05	.03	.02
18.84+	1	18.84	14.91	11.39	7.00	.87	4.80	2.81	2.75	1.17	2.78

Table 4. Continued.

Size Range	Number of Specimens	Lengths						Depths			
		Total	Standard	Preanal	Predorsal	Snout	Head	Head	Body	Eye Diameter	Head Width
20.10+	1	20.10	15.91	12.06	7.41	.89	5.22	3.37	3.33	1.35	3.00
23.37+	1	23.37	17.84	13.99	8.73	1.01	5.70	3.94	3.98	1.57	3.45

+ Denotes only a single observation in this length category.

* Denotes standard error of less than .01.

By 7.5 mm the head was flattened and elongate, the body was slender, the eye was distinctly elliptical, and the single ovoid gas bladder had filled. Between 7.6 and 7.8 mm, the yolk sac was absorbed and feeding commenced. The dorsum of the head had become very depressed. The opercle covered the first gill arch. By 8.2 mm the upper jaw was even with the upper edge of the orbit and remained so throughout the protolarval phase.

Basal supports for caudal fin rays were present by 8.6 to 8.8 mm but rays did not form until 9.1 mm. The apex of the forming dorsal fin was evident over the 15th to 17th preanal myomere.

Pigmentation. At one day posthatching (5.6 mm), the eye was darkly pigmented. A diffuse line of melanophores extended along the ventral midline. Three to five melanophores were present along the nape. By 6.0 mm, a double dorsal row of melanophores was present from the occiput to a point about halfway along the dorsum, and by 6.9 mm the two rows were present to the caudal fin base. Three or four melanophores were present midlaterally just posterior to the head. A concentration of melanophores was situated over the incipient air bladder tissue. The head was heavily covered with large melanophores and the cheeks were becoming pigmented. A line of melanophores was present along the entire dorsum of the gut.

A ventral diffuse row of melanophores was present to the urostyle. The caudal finfold was pigmented just above the urostyle. The ventral midline pigment was aligned in two distinct rows along the yolk sac and gut by 7.5 mm. By the mesolarval phase these lines had become a single diffuse row. The dorsal and ventral postanal melanophores were continuous around the urostyle.

The snout and ventrum of the brain case were pigmented. Heavy pigment extended from the base of the brain case to the dorsum of the gas bladder. Appearing as a "stitched" line, a midlateral row of melanophores extended from the cleithrum to the caudal peduncle. The gill arches were lined with melanophores. A ventral caudal spot formed just anterior to the tip of the urostyle by 8.0 mm. A concentration of melanophores was present at the base of each pectoral fin.

Mesolarvae

Specimens ranged from 9.1 to 16.2 mm. Means of morphometric data are presented in Table 4. Modal numbers and ranges of preanal, postanal, and total myomeres for mesolarvae (41 specimens) were 28 (26-29), 7-8 (5-10), and 35 (32-37), respectively.

Morphology. The opercle covered all the gill arches by 10.9 mm. The urostyle had angled up with the beginning of caudal ray formation and reached its greatest angle by 10.9 mm at which size the hypural complex was complete. The caudal fin was truncated at this size and bilobed by 13.2 mm. The adult complement of caudal fin rays (18) was present by 12.7 mm.

Dorsal rays appeared by 11.4 mm. By 15.6 mm the dorsal, caudal, and anal finfolds had separated. The adult complement of dorsal fin rays (25-28) was present by 16.6 mm. Anal rays appeared between 11.2 and 11.7 mm. The adult complement of anal rays (8-9) was present on specimens larger than 16.2 mm.

Pectoral rays appeared between 10.9 and 11.0 mm. Six to eight rays formed by 11.7 mm. The pelvic fins were present as thin

flanges on the ventral body wall at 12.7 mm. Pelvic rays formed and the fins had grown out even with the distal edge of the ventral finfold by 14.6 mm. Pectoral and pelvic fin ray development was not completed in the mesolarval phase.

The second gas bladder began as an anterior tubular diverticulum of the posterior air bladder chamber between 10.7 and 11.0 mm. Two distinct gas bladders were apparent by 11.4 mm. By 14.1 mm the gut began to bend and one full coil was present by 14.6 mm. Unlike its congeners, the intestines of all highfin carpsucker specimens had coiled to the right hand side of the body.

The mouth began migrating ventrally at about 19.4 mm and consequently became progressively less oblique on larger specimens. By 10.5 mm the edge of the upper jaw was at a level with the middle of the orbit and even with the lower edge of the orbit by 12.5 mm. Near the end of the mesolarval phase (14.6 to 16.2 mm), the mouth was beginning to become subterminal.

Pigmentation. A patch of scattered melanophores on the foregut was present just anterior to the origin of the ventral finfold by 9.7 mm. Along the ventral finfold to the anus was a diffuse row of melanophores. By 10.5 mm the orbit was "stitched" with small melanophores ventrally and posteriorly. Heavy internal pigment was present on the foregut by 14.6 mm.

Melanophores were spread dorsally and ventrally along the myoseptae from the midlateral line of pigment. Lateral body pigment was moderate to heavy by 15.6 mm. The dorsolateral area had the densest concentration of melanophores.

Metalarvae

Specimens ranged from 16.6 to 18.8 mm. Morphometric information is presented in Table 4. Only two specimens were preserved in this phase.

Morphology. By the beginning of the metalarval phase (approximately 16.6 mm), the mouth had become subterminal. The head angled down smoothly from the origin of the dorsal fin to a point over the nares and then angled down sharply along the snout. Fourteen pectoral and eight pelvic rays were already present by the beginning of this phase. The remaining median finfold was confined to the preanal ventral midline. The adult complements of pectoral (16-17) and pelvic (10-11) rays were attained and the median finfold absorbed by 20.1 mm.

Pigmentation. Lateral body pigmentation increased during the metalarval phase. Melanophores below the midlateral line were still confined along the myoseptae. Ventrolateral pigment below the level of the gas bladder was scattered and sparse. External ventral pigment was lacking on the foregut. The ventrum of the mouth and opercle was moderately pigmented. The snout, upper and lower jaws, and dorsum of the head were heavily pigmented. The densest concentration of melanophores was a roughly triangular patch over the midbrain. The double dorsal rows of large melanophores were almost masked by the dense pigment around the rows. Ventrally a double row of melanophores outlined the anal fin base and continued posteriorly as a diffuse single row to the caudal fin.

Caudal and dorsal fins were pigmented to the edges. Anal and pectoral fins had three or four proximal melanophores, and pelvic fins were unpigmented.

Juveniles

Four specimens of juveniles ranged from 20.2 to 36.2 mm. Morphometric data for juveniles are presented in Table 4 (page 34). Ranges and modes of fin ray counts are given in Table 2 (page 20).

Morphology. The characteristic deep "slab sided" appearance of the highfin carpsucker was apparent in early juvenile specimens. The greatest body depth was at the origin of the dorsal fin. The head was bluntly squared off just anterior to the nares. The mouth remained subterminal. The posterior edge of the lips, when viewed laterally, was forward of the anterior edge of the orbit.

Squamation was not apparent on 20.2 mm and 23.3 mm specimens. By 29.3 mm scales had formed only along the peduncle and forward along the midline to the cleithrum. Squamation was complete on the 36.2 mm specimen.

Pigmentation. Patterns of pigmentation resembled that described for metalarvae. Ventrolateral pigment increased. Ventral pigment was still lacking on the foregut and was light elsewhere on the ventrum. Scales were outlined with melanophores but not as conspicuously as those of the quillback or river carpsucker juveniles.

Behavior

The description of behavior was compiled from observations on young of the river and quillback carpsuckers. Embryos began

intermittent rolling in the eggs during the late incubation period. Larvae hatched tail first by means of jerky writhing motions. Often the egg membranes appeared to disintegrate around embryos, probably due to sudden changes in internal pressure when the egg membranes ruptured.

Larvae were negatively rheotactic upon hatching. Newly hatched protolarvae actively swam up head first with the flow of current out of the McDonald hatching jars. Swimming movements were rapid with intermittent periods of sinking for a second or two. By six to eight hours after hatching, larvae were positively rheotactic. They were actively attempting to orient and maintain themselves against the flow-through current in the holding containers. Swimming movements were much more efficient. Larvae maintained themselves in the water column near the surface by one day posthatching.

Denser aggregations of larvae were observed in areas of the containers but could have been due to the hydraulics of waterflow in the tanks. One-week-old larvae (7.6 mm river carpsuckers; 9.7 mm quillback carpsuckers) were proficient swimmers and definitely exhibited schooling behavior, much like buffalo (Ictiobus) larvae. Larvae and juveniles, to the largest sizes cultured, exhibited schooling and were positively rheotactic under moderate to strong currents.

The general activity level of larvae increased in response to the introduction of food. All larvae fed up in the water column until the mouth had migrated to a ventral position. Strict bottom feeding behavior began at about 20 mm for the river carpsucker and 19 mm for the quillback carpsucker. Larvae and juveniles were generally up in the water column until food was introduced. Within a few seconds all young would be actively feeding along the bottom of the tanks.

III. DIAGNOSIS

Eggs

All eggs were spherical and adhesive. No significant differences exist among the egg diameters of the three species of carpsuckers. The eggs of carpsuckers (Carpiodes) are not separable from those of the buffalos (Ictiobus) on the basis of size. The range of egg diameters for members of the subfamily Ictiobinae are less than and mutually exclusive from those of: Cycleptus elongatus, Hypentelium nigricans, Moxostoma carinatum, M. erythrurum, and M. macrolepidotum (Figure 2).

The ranges of egg diameters of Erimyzon oblongus, the creek chubsucker, and Minytrema melanops, the spotted sucker, are similar to those of the carpsuckers. Fuiman (1978) showed the range of egg diameters for Carpiodes cyprinus and E. oblongus in his study to be mutually exclusive. This study corroborates that finding. However, the ranges of egg diameters of the river carpsucker (1.7 to 2.1 mm) and highfin carpsucker (1.9 to 2.0 mm) overlap the range for the creek chubsucker (1.6 to 2.0 mm, Fuiman 1978). The ranges of egg diameters of all three carpsuckers overlap that of the spotted sucker. The range for Catostomus commersoni overlaps the upper range of the carpsuckers, but the mean and one standard deviation of the mean for the white sucker (Fuiman 1978) did not overlap the carpsucker range.

Protolarvae (Figures 3-5)

Total lengths, at which selected morphological changes occurred, appear in Table 5. The mean hatching size of the three

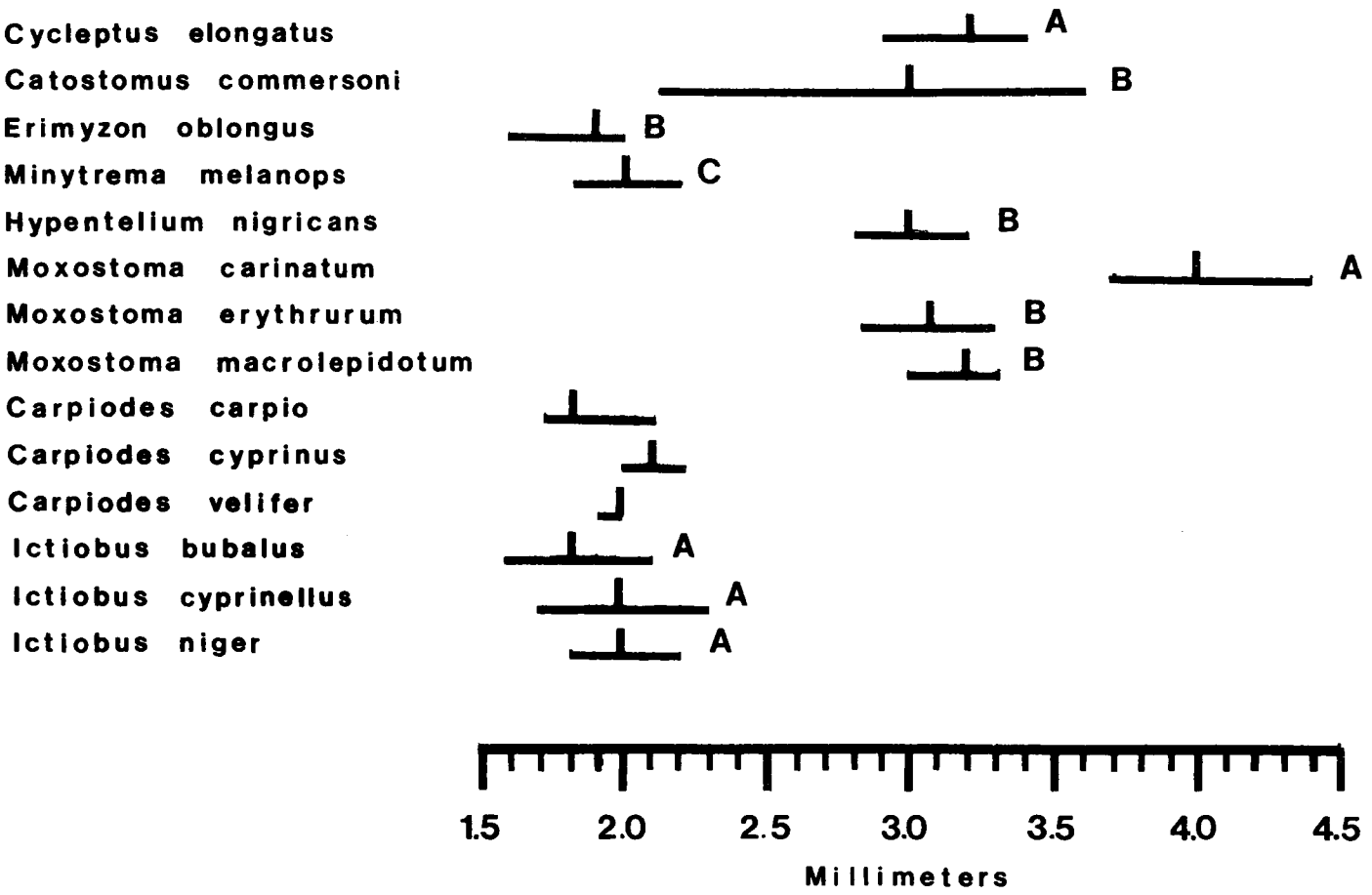


Figure 2. Ranges and means of egg diameters of the three species of carpsuckers and representatives of other catostomid genera. (Source: A. Yeager, unpublished data; B. Fuiman 1978; C. Hogue and Buchanan 1977).

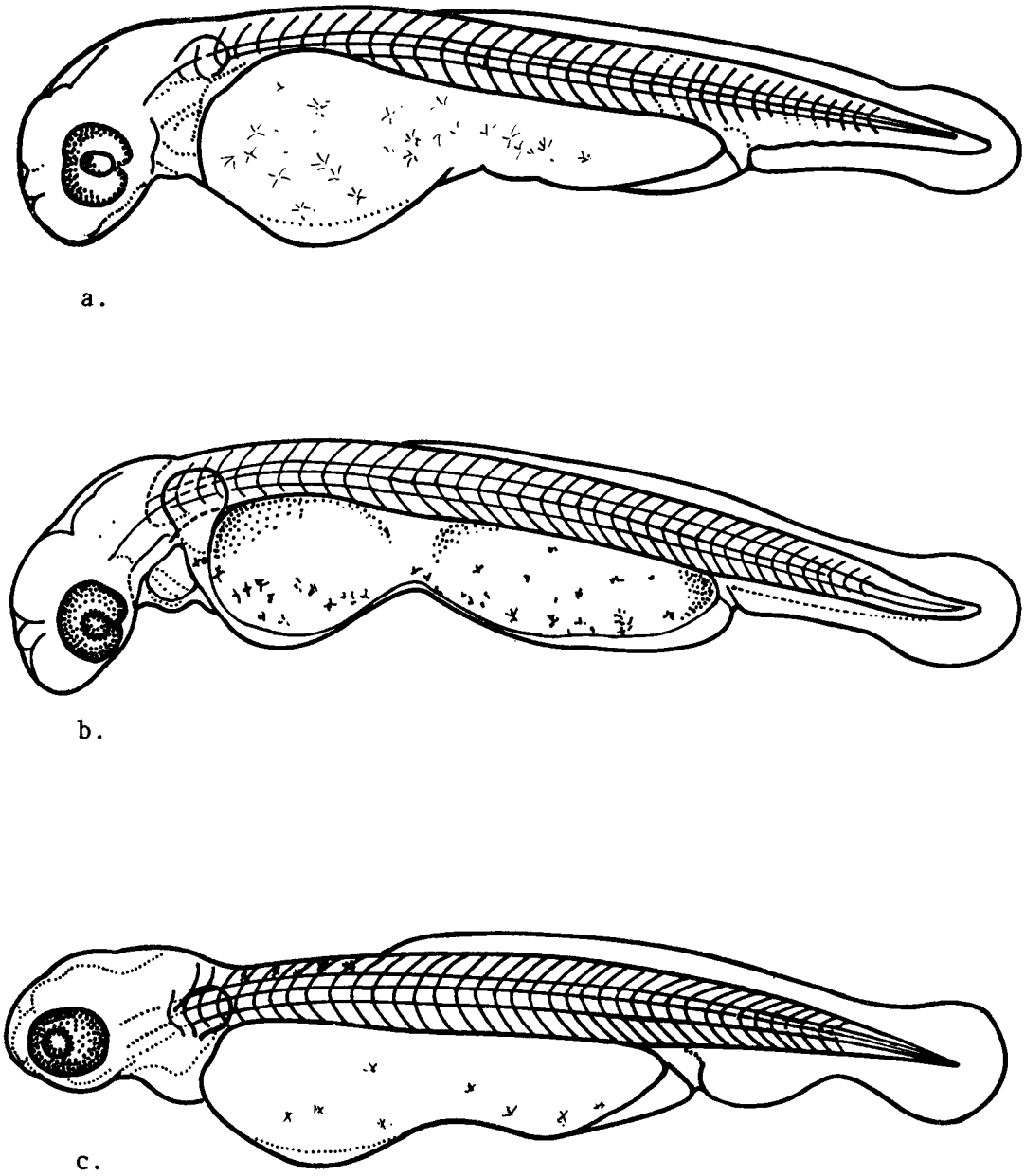
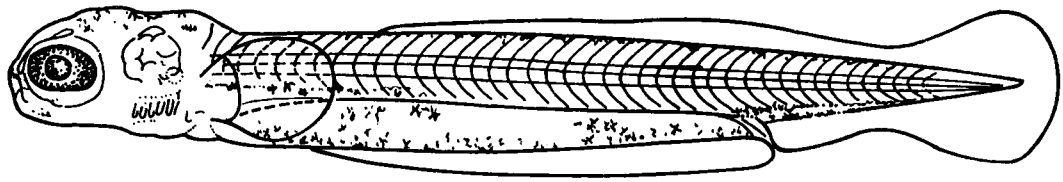
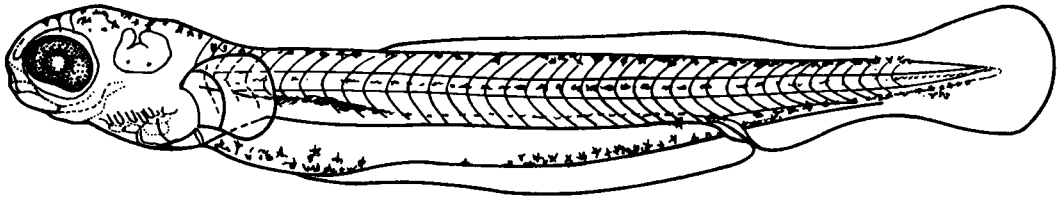


Figure 3. Protolarvae: a. river carpsucker at hatching, 5.2 mm TL; b. quillback carpsucker at hatching, 6.5 mm TL; c. highfin carpsucker one day posthatching, 5.6 mm TL.



a.



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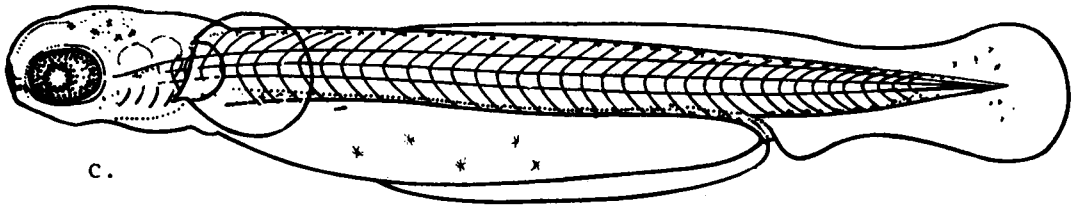
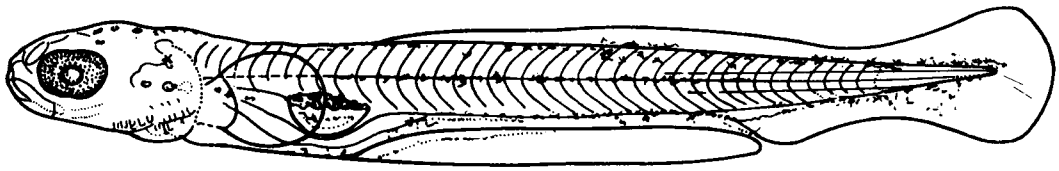
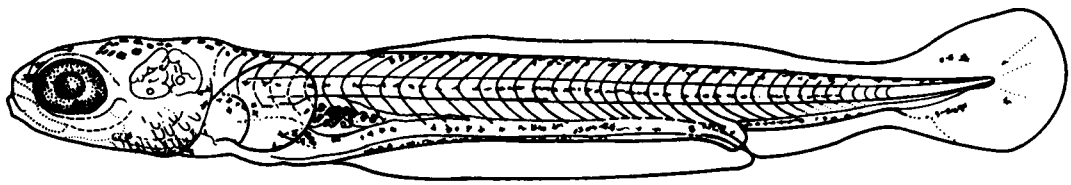


c.

Figure 4. Protolarvae: a. river carpsucker, 7.6 mm TL; b. quillback carpsucker, 8.9 mm TL; c. highfin carpsucker 7.2 mm TL.



a.



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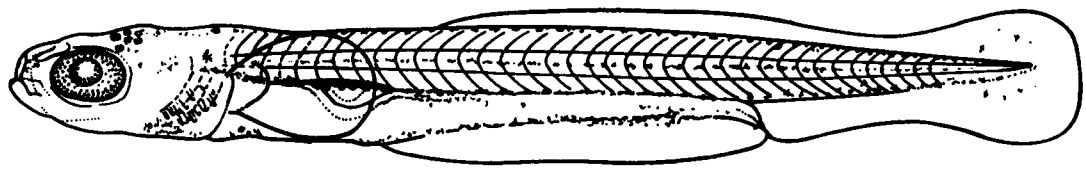


c.

Figure 5. Protolarvae: a. river carpsucker, 8.3 mm TL; b. quillback carpsucker, 9.9 mm TL; c. highfin carpsucker, 8.0 mm TL.

Table 5. Total length (in millimeters) at which selected morphological changes occur during development of the three species of carpsuckers.

Species	Carpiodes carpio	Carpiodes cyprinus	Carpiodes velifer
Mean Hatching Size	5.3	6.5	<5.6
Terminal Mouth	7.6-8.0	8.8- 9.7	6.9
Subterminal Mouth	20.2	18.8	16.2
Flattened Head	7.7	8.6	7.5
Presence of:			
1st Gas Bladder	7.7	8.6- 9.2	7.5
2nd Gas Bladder	14.2-14.6	14.4	11.4
Yolk Sac Absorbed	7.7- 8.2	9.1- 9.6	7.6- 7.8
Gut Coiling Begins	12.8-13.4	16.4-17.1	14.1
One Full Gut Coil Present	13.8-16.1	16.4-17.1	14.6
Protolarval Phase	5.0-11.0	5.8-11.0	5.4- 9.1
Mesolarval Phase	9.7-19.3	10.0-20.6	9.1-16.2
Metalarval Phase	19.1-23.4	19.7-25.6	16.6-18.8
Juvenile Period	22.8-?	24.4-?	20.2-?

Table 5. Continued.

Species	Carpiodes carpio	Carpiodes cyprinus	Carpiodes velifer
Beginning/Completion of Fin Ray Development			
Caudal	9.7-10.2/14.2-14.7	10.0-11.0/15.5	9.1-9.4/12.7
Dorsal	12.5-13.4/19.1-19.3	14.2-15.1/19.7-20.6	11.4/16.6
Anal	15.6-16.1/17.7-19.4	16.4-16.9/19.7-20.6	11.2-11.7/16.2
Pectoral	13.8-14.2/22.3-23.1	16.4-17.1/22.8-23.9	10.9-11.0/20.1
Pelvic	16.9 /20.9-22.8	17.6-19.2/21.6-22.3	14.6 /20.1
Pelvic Fin Buds Present	12.3	12.0-12.7	12.7

species ranged from 5.3 mm for the river carpsucker to 6.5 mm for the quillback carpsucker (Table 5). A hatching size roughly comparable to that of the river carpsucker may be inferred for the highfin carpsucker, which was 5.6 mm at one day posthatching.

Modal preanal and total myomeres for protolarvae of C. velifer were 29 (26-29) and 37 (35-39), respectively. For C. carpio, modal numbers of preanal and total myomeres were 30 (29-31) and 38 (36-39), respectively. Modal preanal and total myomeres for the quillback carpsucker were 31 (28-32) and 40 (37-42), respectively.

The cumulative distribution of preanal, postanal, and total myomeres for the three species of carpsuckers at all phases is shown in Table 6. From information in the recent literature or observations on undescribed larval material of Cycleptus elongatus, Catostomus commersoni, Erimyzon oblongus, Hypentelium nigricans, Minytrema melanops, Moxostoma carinatum, M. erythrurum, M. macrolepidotum, Ictiobus bubalus, I. cyprinellus, and I. niger the following diagnostic information is notable (Table 7, Figure 6). The best discriminating character between the subfamilies Cycleptinae, Catostominae, and Ictiobinae involves numbers of preanal myomeres. Cumulative ranges of preanal, postanal, and total myomeres of undifferentiated phases for the subfamilies Ictiobinae and Catostominae were presented by Snyder (1979). Cycleptus elongatus, the only member of the Cycleptinae, has 37-43 preanal, 10-14 postanal, and 47-54 total myomeres (Hogue et al. 1979), respectively. Some overall range overlap exists but cumulative modal ranges of preanal myomeres for the species of the three subfamilies are quite distinct (Figure 6).

Table 6. Cumulative frequency distribution of preanal, postanal and total myomeres of the carpsuckers expressed as percentage of total observations (N). Includes protolarval, mesolarval, and metalarval carpsucker data.

	Preanal Myomeres							
Species	26	27	28	29	30	31	32	N
Carpiodes carpio		1	6	46	41	6		160
C. cyprinus			11	23	33	31	3	160
C. velifer	6	23	43	29				84

	Postanal Myomeres							
Species	5	6	7	8	9	10	11	N
Carpiodes carpio	2	36	25	21	16	<1		160
C. cyprinus	6	26	13	11	29	14	3	160
C. velifer	4	13	21	40	21	1		84

	Total Myomeres											
Species	32	33	34	35	36	37	38	39	40	41	42	N
Carpiodes carpio			4	28	14	17	34	4				160
C. cyprinus			8	20	13	6	6	12	28	8	1	160
C. velifer	5	4	13	21	27	24	5	1				84

Table 7. Modal numbers and ranges of preanal, postanal, and total myomeres for the three species of carpsuckers and representatives of other catostomid genera. Mode (range).

	Preanal Myomeres		Postanal Myomeres		Total Myomeres		Source
Cycleptus elongatus	41	(37-43)	11	(10-14)	53	(47-54)	A. Hogue (In Press), Hogue unpublished data
Catostomus catostomus	38	(36-40)	9	(5-12)	47	(44-50)	B. Fuiman and Whitman 1979
C. commersoni	38	(35-42)	8	(5-13)	46	(42-52)	C. Fuiman 1978
Erimyzon oblongus	31	(30-33)	9	(7-10)	40	(38-42)	C.
Minytrema melanops[+]	34, 33	(31-35)	6, 8	(4- 7)	40, 41	(35-42)	D. Hogue and Buchanan 1977
Hypentelium nigricans	37	(33-40)	9	(3-11)	46	(39-49)	C.
	#38, 35, 34	(33-38)	5, 7, 7	(5- 8)	43, 42, 41	(40-44)	E. Buynak and Mohr 1978
Moxostoma carinatum	35	(33-38)	6	(5- 8)	41	(39-46)	F. Yeager, unpublished data
M. erythrurum	34	(31-37)	7	(6- 9)	41	(39-45)	B.
	35	(32-37)	6	(5- 8)	41-42	(38-44)	F.
M. macrolepidotum	36	(35-39)	8	(5- 9)	44	(42-46)	C.
	#35, 34, 32	(30-35)	6, 6, 7	(5- 8)	40, 41, 41	(38-41)	G. Buynak and Mohr 1979

Table 7. Continued.

	Preanal Myomeres		Postanal Myomeres		Total Myomeres		Source
Carpiodes carpio	29	(27-31)	6	(5-10)	38	(34-39)	H. Cumulative data from Table 6
C. cyprinus	30	(28-32)	9	(5-11)	40	(34-42)	H.
C. velifer	28	(26-29)	8	(5-10)	36	(32-39)	H.
Ictiobus bubalus	30	(28-31)	8	(5- 9)	38	(33-39)	F.
I. cyprinellus	29	(28-31)	8	(5- 9)	37	(34-39)	F.
I. niger	29	(28-31)	8	(6-10)	38	(35-40)	F.

+ Prolarvae, postlarvae (cumulative range).

Protolarvae, mesolarvae, metalarvae (cumulative range).

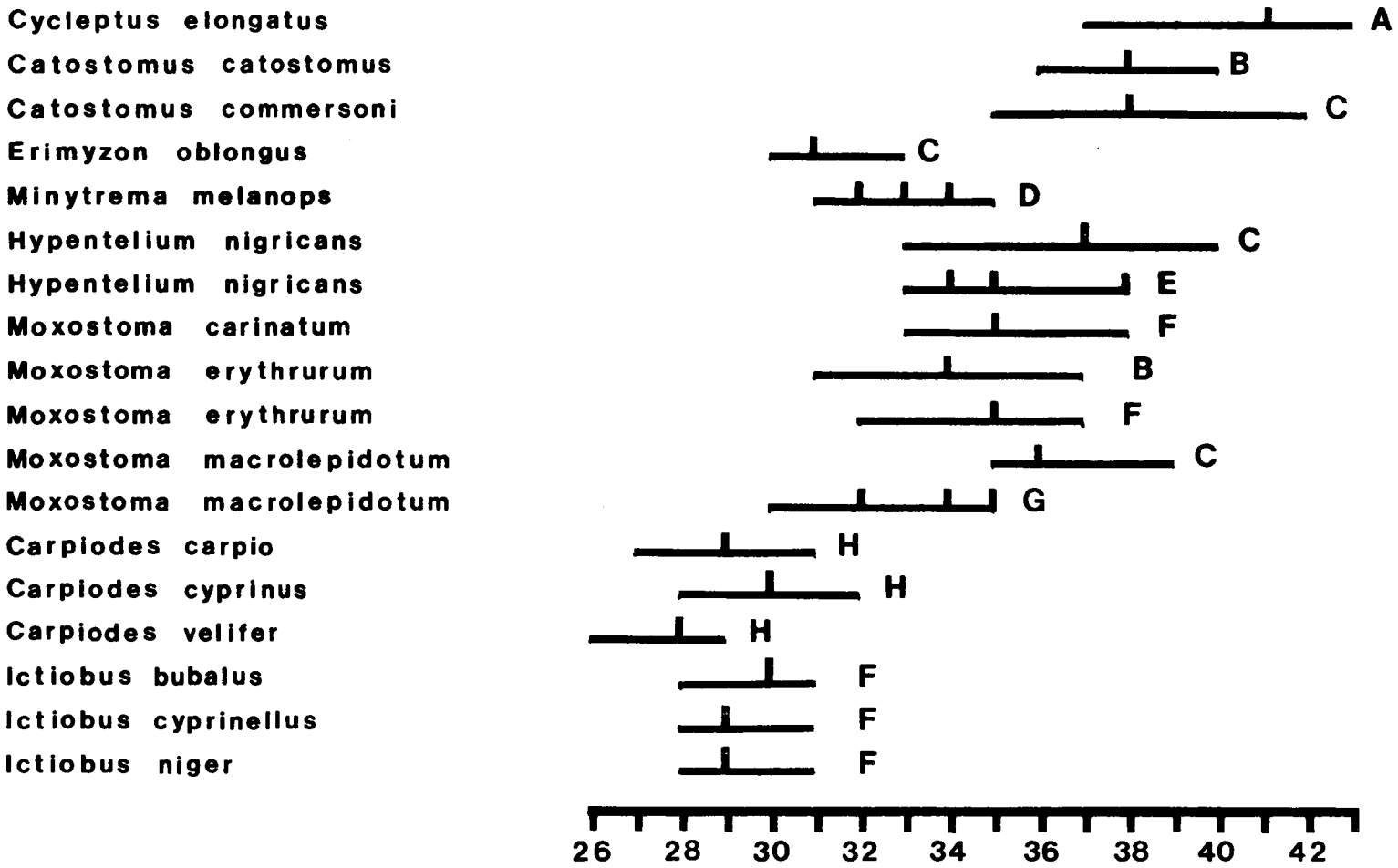


Figure 6. Ranges and modal numbers of preanal myomeres of the three species of carpsuckers and representatives of other catostomid genera. (Sources: Table 7).

Snyder (1979) indicated cumulative modal ranges for five species of unspecified Ictiobinae to be 26-31 preanal, 7-9 postanal and 33-38 total myomeres, respectively. Within the Ictiobinae, the modal numbers of preanal myomeres (Figure 6) are too similar to use independently for discriminating species.

Until the characteristic flattening of the head by 7.5 to 8.6 mm and formation of the elliptical eye at 7.7 to 8.6 mm protolarval carpsuckers are very difficult to identify from buffalo larvae. However, early protolarval pigmentation on the yolk sac of buffalos is confined to an intensified, irregular midventral line of melanophores. Yolk sac pigmentation of the carpsuckers is usually much more widespread laterally. After dorsal pigmentation patterns are established, creek chubsucker larvae, unlike carpsuckers, have three dorsal rows of pigment and a broad pigment-free area located medially along the occiput (Fuiman 1978). The modal number of preanal myomeres (31) is also higher for the creek chubsucker than for the river and highfin carpsuckers.

Of the carpsuckers the highfin carpsucker was most precocious in development (Table 5). The river carpsucker was generally more precocious than the quillback carpsucker. Characteristic dorsal pigment patterns (e.g., double dorsal row of melanophores and heavy head pigment) were established at smaller total lengths on the river and highfin carpsuckers than on the quillback carpsucker. Results of analysis of variance of morphometric data on pairs of carpsucker species are presented in Tables 8, 9, and 10 as a tool for ichthyoplankton taxonomists.

Table 8. Results of one-way analysis of variance of selected characters for the river and quillback carpsuckers expressed as probabilities of random occurrence (Significant probability P≤.05).

Size Class (Total Length mm)	Lengths					Depths			
	Standard	Preanal	Predorsal	Snout	Head	Head	Body	Eye Diameter	Head Width
6	.075	.138	*	.007	.782	.304	*	.259	.290
7	.692	.547	.002	.001	*	.010	.072	.402	.014
8	.232	.092	.006	*	*	.386	*	*	*
9	.768	.395	.001	.024	*	.001	*	.023	*
10	.104	.028	*	*	*	*	*	.022	*
11	.012	.593	.008	.390	.125	.004	.009	.021	.001
12	*	.033	.008	.023	.456	.002	.002	.006	*
13	*	.345	.001	*	.018	.007	*	.573	.001
14	.039	.629	.053	.045	.153	.012	*	*	.008
15	.233	.625	*	.007	.008	.001	.003	.001	*
16	.490	.546	.008	.021	*	.383	*	*	*
17	.197	.003	*	.259	.001	.009	*	.013	.002
18	.914	.066	.035	.052	.009	.104	*	.063	.061
19	.071	.050	.185	.137	.033	.046	*	.002	.083
20	.001	.001	.257	.082	.013	.009	*	.054	.374
21	.263	.766	.341	.011	.335	*	*	.003	.510
22	.026	.002	.114	.033	.528	.002	*	*	.865
23	.212	.067	.240	.070	.808	.005	.008	*	.004
24	.027	.002	.551	.161	.353	.003	.527	*	.191
25	.041	.024	.002	.247	.715	.001	.926	*	.149

* Denotes Probability P<.001.

Table 9. Results of one-way analysis of variance of selected characters for the river and highfin carpsuckers expressed as probabilities of random occurrence (Significant probability P≤ .05).

Size Class (Total Length mm)	Lengths					Depths		Eye Diameter	Head Width
	Standard	Preanal	Predorsal	Snout	Head	Head	Body		
6	.298	.918	.049	.001	.334	.067	*	.089	1.000
7	.600	.648	.833	.659	.941	.114	.007	.291	.697
8	.141	.167	.246	*	*	.011	.009	.006	.752
9	.047	.059	.089	.001	.967	*	.001	.360	.002
10	.680	.295	.854	*	.109	.781	.440	.660	.572
11	*	.006	.883	*	.001	.111	.114	.111	.070

* Denotes Probability P<.001.

Table 10. Results of one-way analysis of variance of selected characters for the quillback and highfin carpsuckers expressed as probabilities of random occurrence (Significant probability P≤.05).

Size Class (Total Length mm)	Lengths					Depths			
	Standard	Preanal	Predorsal	Snout	Head	Head	Body	Eye Diameter	Head Width
6	.623	.298	.038	*	.547	.028	.525	.248	.255
7	.467	.385	.006	.029	*	.397	.139	.851	.037
8	.896	.743	*	*	*	.111	.023	*	*
9	.039	.335	.012	*	*	.020	.019	.014	*
10	.249	.334	*	*	*	*	*	.012	*
11	*	.027	.037	*	.072	.135	.072	.255	*

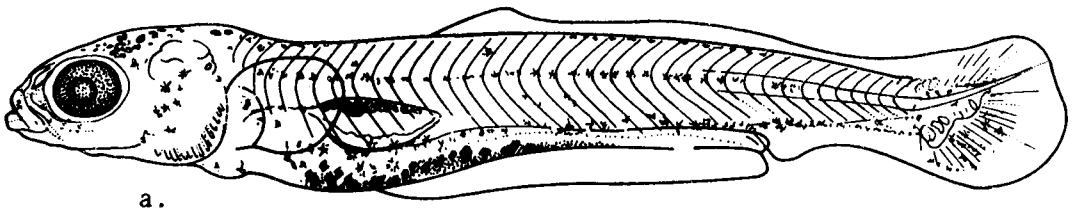
* Denotes Probability P<.001.

Mesolarvae (Figures 7-9)

As discussed for protolarvae, numbers of preanal myomeres (Table 7, Figure 6) continued to be of diagnostic value in identifying Carpiodes from larvae of other catostomid species except Ictiobus spp. and Erimyzon oblongus. Mesolarval carpsuckers are easily separated from Ictiobus larvae (Yeager, unpublished descriptions), which lack the elliptical eye, flattened head, and more slender body of the carpsuckers. The aforementioned pigment-free area on the occiput, broad midlateral stripe, and smaller size at particular stages of development (Fuiman 1978) serve to adequately separate Erimyzon oblongus from Carpiodes spp. in the mesolarval phase.

Within the genus Carpiodes, species definition is possible using a combination of modal numbers of preanal myomeres, head shape, and total length at particular stages of development (Table 5). Modal numbers of preanal myomeres for hatchery cultured river, quillback, and highfin carpsucker larvae were: 29, 29-30, and 28, respectively. Results of analysis of variance of morphometric data including mesolarvae are shown in Tables 8, 9, and 10.

In the early mesolarval phase, subtle head-shape differences were apparent which became more notable throughout mesolarval and metalarval development. By 10.2 mm the head of the river carpsucker sloped down from a point just over the second gill arch, and over the posterior one-third of the eye was an indentation of the dorsal profile of the head. The dorsum of the head of the quillback carpsucker rounded down smoothly from the occiput to the tip of the snout. Though the head sloping began more posteriorly as on the quillback carpsucker,



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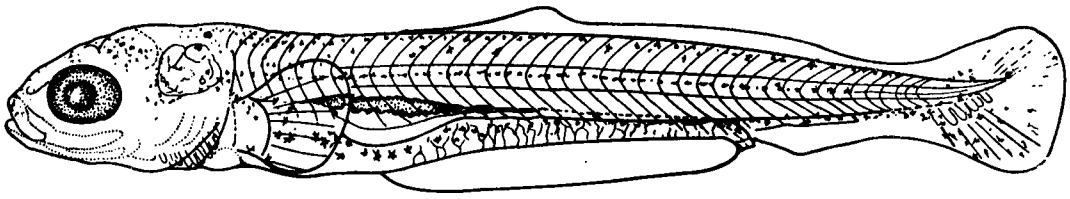

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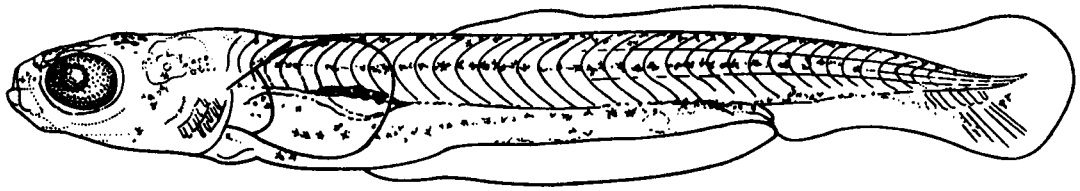
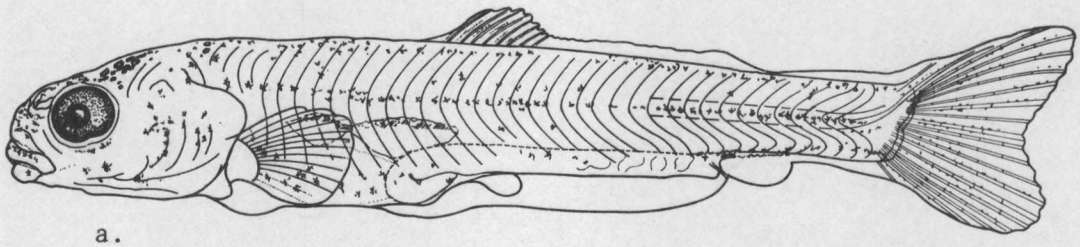


c.

Figure 7. Mesolarvae: a. river carpsucker, 11.4 mm TL; b. quillback carpsucker, 11.4 mm TL; c. highfin carpsucker, 9.3 mm TL.



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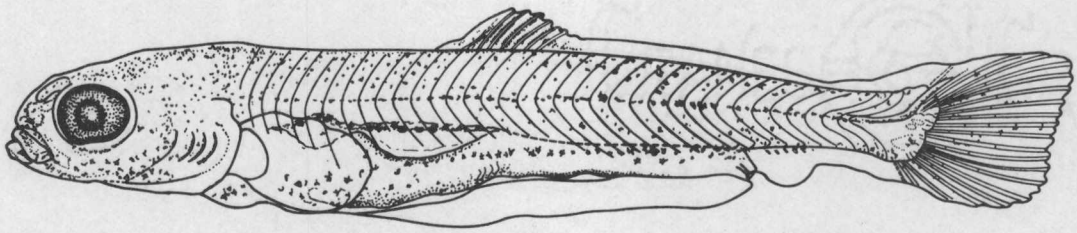

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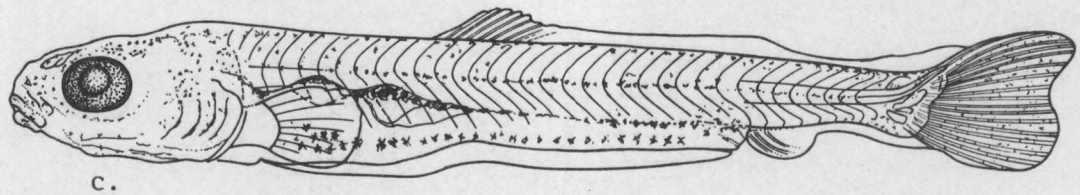

c.

Figure 8. Mesolarvae: a. river carpsucker, 15.1 mm TL; b. quillback carpsucker, 15.1 mm TL; c. highfin carpsucker, 11.5 mm TL.

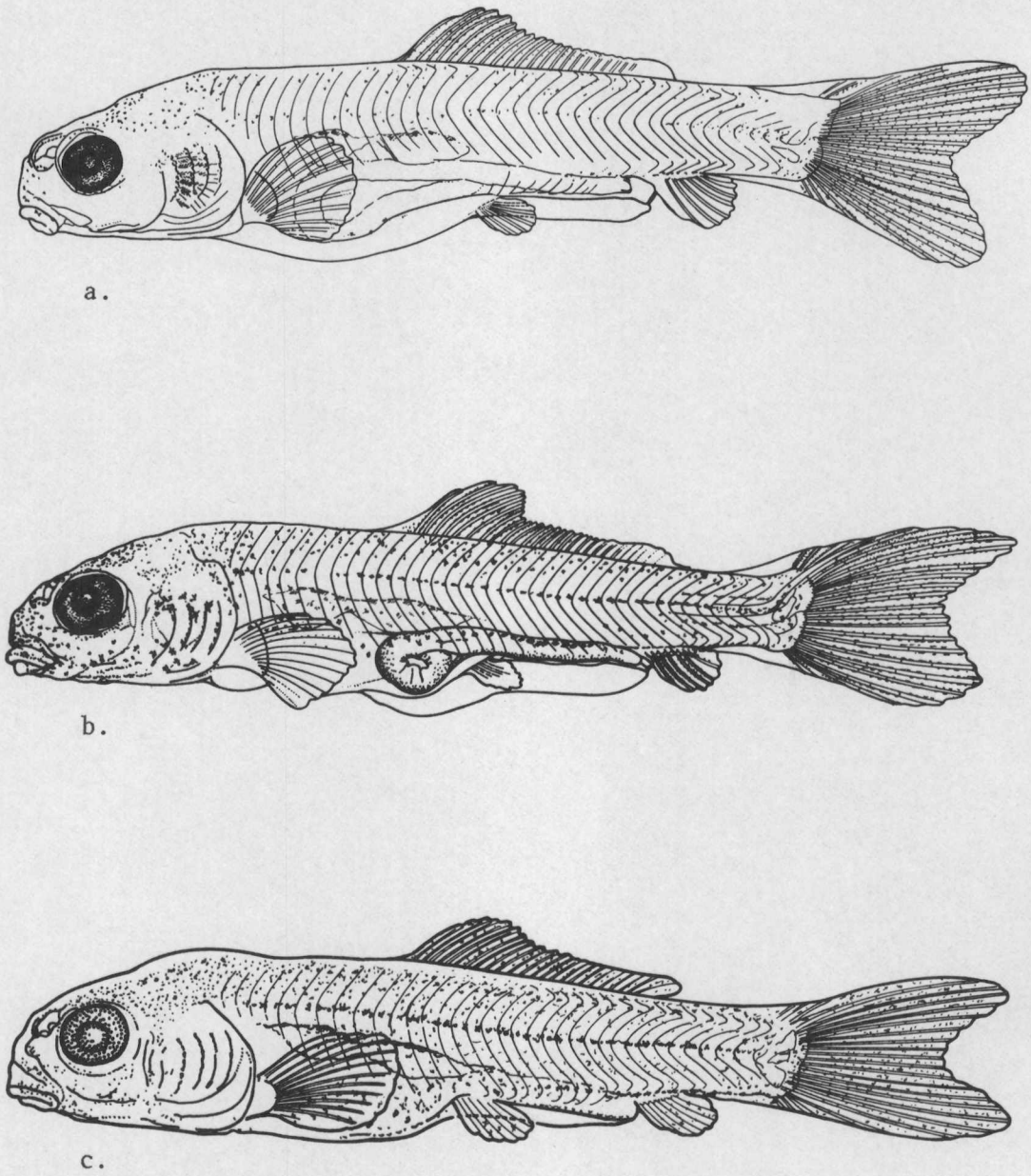

Figure 9. Mesolarvae: a. river carpsucker, 17.6 mm TL; b. quillback carpsucker, 17.8 mm TL; c. highfin carpsucker, 16.2 mm TL.

the head of the highfin carpsucker sloped down much more steeply. On the highfin carpsucker was an indentation of the head dorsum just posterior to the eye.

The original flattening of the head occurred earliest in the highfin carpsucker (Table 5). The highfin carpsucker was the most precocious of the three species in the incipient formation and completion of rays in all fins and formation of the air bladder. The river carpsucker attained comparable stages of these characters at larger total lengths than the highfin carpsucker but smaller than those of the quillback carpsucker.

Berner (1948) described the gut convolutions of Carpiodes and Ictiobus for use as generic characters. Coiling of the gut began at smaller total lengths on the river carpsucker than either the highfin or quillback carpsuckers. The first gut coils of all specimens of the river and quillback carpsuckers formed to the left side of the body. A right hand gut coil formed on all highfin carpsucker material examined. Only a few (10) highfin carpsuckers were available for examination of gut coiling, so this character should be considered tenuous until further study determines the variability, if any, of this condition. The gut coil of the river carpsucker reached a position just posterior to the pectoral fin that was not attained by the quillback carpsucker.

The highfin carpsucker developed a patch of melanophores on the foregut just anterior to the origin of the ventral finfold that was lacking on river and quillback carpsuckers in this phase. Otherwise, pigmentation patterns were very similar.

Metalarvae (Figure 10)

Characteristic head shape differences that were noted for mesolarval carpsuckers were apparent throughout the metalarval phase. The dorsum of the highfin carpsucker sloped down smoothly from the origin of the dorsal fin to a point just over the nares and then angled down sharply. The head of the quillback carpsucker was relatively smoothly sloped from the occiput to the tip of the snout. The characteristic depression in the dorsum of the head of the river carpsucker was retained in the metalarval phase.

Completion of pectoral and pelvic fin ray development was attained at a smaller total length by the highfin carpsucker than for the other two species (Table 5, page 48). Results of analysis of variance of morphometric data for size classes including metalarvae are shown in Tables 8, 9, and 10.

The external ventral pigment noted on the foregut of the mesolarval highfin carpsucker was lacking in this phase and still not formed on the river carpsucker. However, a variable concentration of melanophores (5-15) was present at the origin of the remaining ventral finfold on the quillback carpsucker. The remainder of the foregut was sparsely pigmented.

Metalarval carpsuckers and buffalos are distinguishable from other catostomids by the long dorsal fin base and associated larger numbers of dorsal fin rays. Carpsuckers and buffalo are identifiable on the basis of the subterminal mouth and flattening of the ventrum of the body profile shown by the carpsuckers. The lower jaw and snout slope evenly to the still terminal mouth of metalarval buffalo (Yeager, unpublished descriptions).

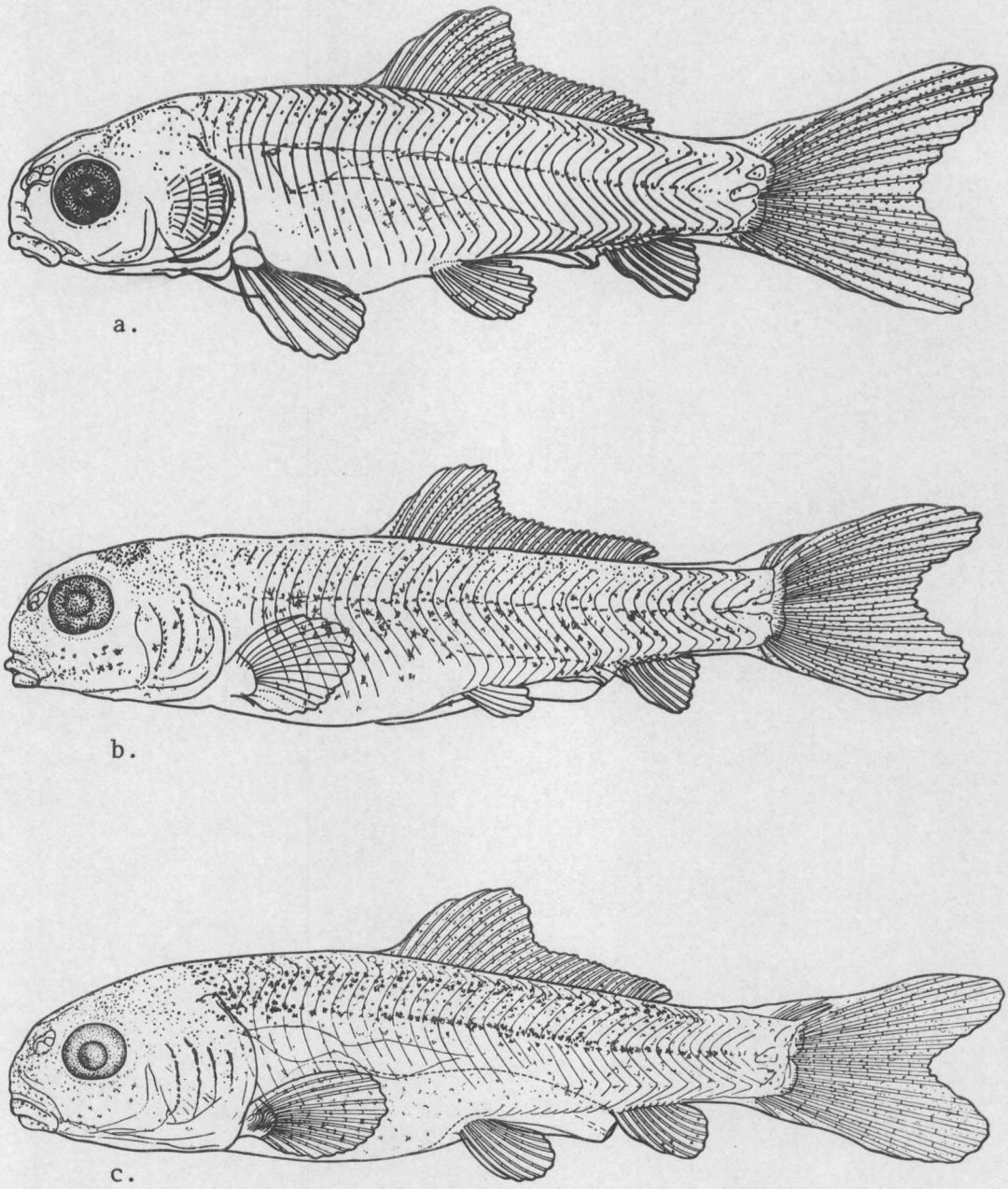

Figure 10. Metalarvae: a. river carpsucker, 21.1 mm TL; b. quillback carpsucker, 21.1 mm TL; c. highfin carpsucker, 18.8 mm TL.

Juveniles (Figure 11)

The attainment of adult fin ray counts in all fins and complete absorption of the median finfold for carpsuckers occurred in the following order: highfin (20.2 mm), river (22.8 mm), and quillback (24.4 mm). Early juvenile carpsuckers appear similar to metalarvae in gross morphology and pigmentation. Characters noted for metalarvae remain usable for early juveniles.

In addition, by 17.5 to 18.0 mm, the position of the subterminal mouth of the river carpsucker differed from the other two species. The posterior edge of the lips of the river carpsucker was situated even with an imaginary vertical line extending dorsally through the anterior edge of the orbit. The posterior edge of the lips of the quillback and highfin carpsuckers were situated more anteriorly. The pelvic fins of the quillback carpsucker were located more posteriorly in relation to the dorsal fin origin than those of the river or highfin carpsucker. The "slab-sided" deeper bodied outline of the highfin carpsucker was already apparent from juvenile specimens 23.3 mm or larger. Results of analysis of variance of morphometric data on early juveniles are shown in Tables 8, 9, and 10.

For all fins, the ranges of numbers of rays was overlapping (Table 2, page 20). Modal differences were observed for the numbers of pelvic rays for the river carpsucker (9) and those for the other two species (10). Modal numbers of dorsal fin rays also differed among the three species (Table 2, page 20).

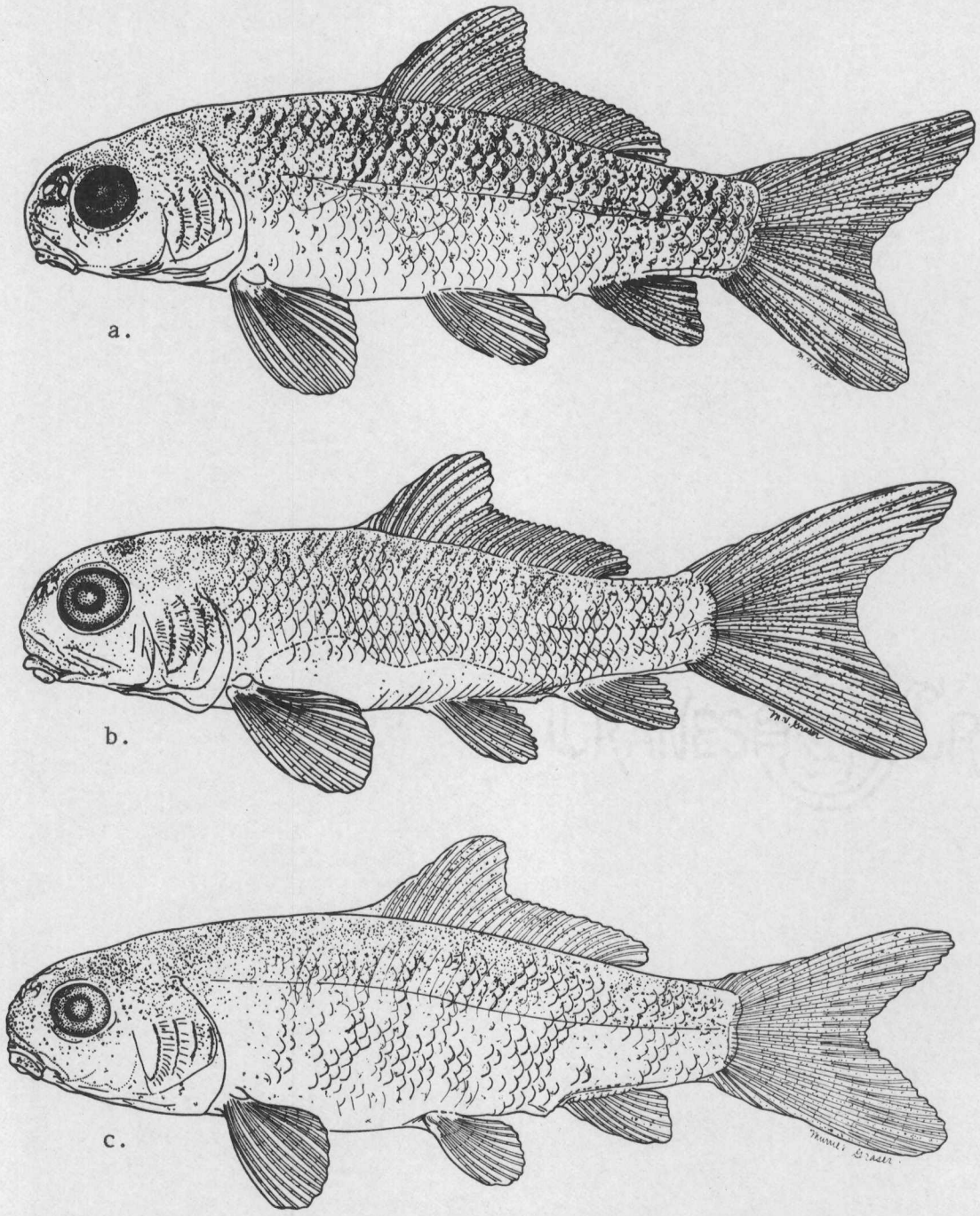

Figure 11. Juveniles: a. river carpsucker, 30.1 mm TL; b. quillback carpsucker, 28.8 mm TL; c. highfin carpsucker, 29.3 mm TL.

IV. DISCUSSION

The identification of carpsucker larvae is possible utilizing a combination of characters in different developmental phases. The Ictiobinae as a group are identifiable on the basis of meristic characters, egg and hatching size, total length at particular stages of development, and pigmentation patterns. Taxonomic separation of carpsucker and buffalo larvae is difficult only in the protolarval phase. However, meristic and pigmentation differences are present in this phase. Head and body morphology are adequate characters for separating the two genera at all other stages.

Identification at the species level within the genus Carpiodes is most tenuous in the protolarval phase. Establishment of pigment patterns, size at developmental occurrences, and significantly different morphometric characters were useful in differentiating protolarvae. Characteristic head and mouth morphology was useful in taxonomy through and beyond the mesolarval phase.

Quillback carpsucker larvae of this study hatched at a greater total length (6.5 mm) than the 5.5 mm reported by Gerlach (1973). Developmental events occurred at greater total lengths than those found in her study (e.g., this study vs. Gerlach [1973]): filling of the gas bladder, 8.6 mm vs. 6.6 mm; yolk sac absorbtion, 9.1 mm vs. 7.0 mm; formation of caudal rays 10.0 mm vs. 9.0 mm; presence of a distinct two chambered gas bladder, 14.4 mm vs. 12.0 mm; appearance of dorsal rays, 14.2 mm vs. 12.0 - 13.9 mm; and appearance of anal fin rays, 16.4 mm vs. 13.0 - 15.9 mm). Those size classes reported by Fuiman (1978)

for developmental occurrences of quillback larvae were intermediate between those of this study and those of Gerlach (1973). The total length at which particular developmental events occur thus appears to vary geographically. Trautman (1957) recognized two subspecies of C. cyprinus. The geographical distribution of C. cyprinus cyprinus, the eastern quillback carpsucker, includes the study areas of Gerlach (1973) and Fuiman (1978). The distribution of C. cyprinus hinei, the central quillback carpsucker, encompasses the area from which broodstock of this study were taken. Whether these differences in larval development support this division, are population characteristics, or result from environmental influences on development is not known.

First coiling of the gut occurred at approximately the same size in each study. Pelvic fin buds appeared earlier on specimens of this study. Gerlach (1973) reported and Fuiman (1978) restated that the dorsal median finfold arose at the eighteenth preanal myomere. The median finfold of the quillback larvae of this study originated at the tenth to twelfth preanal myomere. The 21-mm specimen figured by Fish (1932) corresponded to comparably sized metalarvae of this study.

Morphometric data were analyzed by millimeter class size in order to minimize effects of allometric growth exhibited by fish larvae. Fuiman (1978) found that, grouped in Snyder's (1976) descriptive phases, his data were "not entirely satisfactory" for taxonomic utility. Standard deviations and standard errors of size classes for the species in this study were consistent and small enough to be reliable though each class was based on fewer specimens. Comparison of the species by pairs was utilized because of the more limited data available for the highfin carpsucker.

The problems associated with the reliability of snout length encountered by Fuiman (1978) were also found by the author. Due to the difficulty in obtaining small accurate measurements and possibility of bias in rounding to discrete values, snout length is not considered usable by the author. Other characters exhibiting significantly different means were considered to be useful taxonomic guidelines. However, as perceivable, when the ranges and standard deviations of characters are observed, much overlap between species exists for individual characters, thus limiting the taxonomic value of simple statistical tests for differences of means of morphometric characters.

Larval evidence corroborates results from biochemical and morphological studies on adults that indicate the subfamily Ictiobinae and the genus Carpiodes are distinct, well defined taxa. The similarity of intra-generic development among the species of Carpiodes, the reflection of close relationship with the genus Ictiobus, and the greater dissimilarity with the development of other catostomid species follows accepted phylogenetic generalities.

From a study of the upper jaw mechanism, Eaton (1935) suggested the derivation of the catostomids from cyprinid-like ancestral stock. Nelson (1948) noted affinities of the catostomids with the cyprinids in the morphology of the Weberian apparatus. On the basis of pharyngeal tooth ontogeny in the genus Catostomus, Weisel (1967) proposed a common ancestor for catostomids and cyprinids. Evidence of a cyprinid-like ancestor is also suggested in cytogenetic research (Uyeno and Smith 1972).

The ranges of total myomeres for many cyprinid genera overlap those of Carpiodes and Ictiobus (Snyder 1979). Fuiman (1978), commenting on similarities between the ictiobine genus Carpiodes and the cyprinid genera Cyprinus and Carassius, noted that the carp, Cyprinus carpio, has a small adhesive egg and 24 or 25 preanal myomeres, approaching the lower range of the Ictiobinae.

The phylogenetic relationships within the Catostomidae have been studied on the basis of morphology and meristics (Hubbs 1930; Krumholz 1943; Nelson 1948, 1949; Miller 1958; Jenkins 1970; Eastman 1977). Hubbs (1930) divided the North American catostomids into three subfamilies: Cycleptinae, Ictiobinae, and Catostominae.

The subfamilies Cycleptinae and Ictiobinae are at the opposite range extremes of numbers of preanal myomeres for catostomids (Figure 6, page 54). A cycleptine ancestor was probably an early offshoot of basal catostomid stock. However, the characters shown by the extant genus Cycleptus, e.g., high scale and vertebral counts, higher numbers of myomeres in larvae (characters generally shown by more lotic-oriented catostomids), and a large pelagic egg, are not necessarily those of the basal ancestral catostomids. These characters could possibly be relicts from a lotic invasion by cycleptine ancestors. Adult Cycleptus prefer river habitats with moderate to strong current during most life history stages and for spawning. Adults do not hold well in tanks or ponds. Determination of the larval characteristics of the related genus Myxocyprinus of China could possibly shed more light on this question. Young of Myxocyprinus are of a Carpiodes-like high-bodied form and do not assume the Cycleptus-like terete form until

adulthood. The Weberian apparatus of Myxocyprinus also has been described as being Carpiodes-like in juveniles and becoming Cycleptus-like in the adult (Nelson 1976). Larval and adult ictiobine characteristics, e.g., low numbers of preanal myomeres in larvae, low numbers of vertebrae, long dorsal fin, and low scale counts, could more closely represent those of ancestral catostomid stocks than those of Cycleptus.

The fossil record for catostomids is incomplete and inconclusive. Modern groups of catostomids are not recognizable until the Miocene (Jenkins 1970). An Eocene fossil catostomid from southeast Asia (Hussakof 1932) is of questionable age and affinities. Amyzon, an Eocene genus (Uyeno and Miller 1963) of catostomids from western North America further complicates interpretation of early catostomid derivation, distribution, and relationships. Amyzon is of a moderately deep-bodied form with a long dorsal fin, but no affinity with extant species has been demonstrated.

Fuiman (1978) suggested a possible closer affinity between Erimyzon and Carpiodes than previously thought based on similarities of larvae. Biochemical evidence (Tsuyuki et al. 1967, Huntsman 1970, Ferris and Whitt 1978) suggests that the tribe Erimyzonini is the closest representative of the subfamily Catostominae to the ancestral ictiobine stock. However, one should be cautious in interpreting phylogenetic relationships from meristic larval characters until more is known about environmental effects on "critical periods" of development in fishes (Vladimirov 1975) or whether advantageous character states are selected for in the embryonic or larval periods. Selective factors in evolution could possibly have great consequences at these "critical

periods." The possibly derived characters of adult chubsuckers, e.g., lower scale counts and incomplete lateralis system, would suggest that the lower preanal counts, small egg diameter, and hatching size of Erimyzon could be due to convergence.

Within the genus Carpiodes, relationships of the three species are not easily discernable on the basis of larval characters. As adults, C. cyprinus is more distinct morphologically than C. carpio and C. velifer (Moore 1957). Based on the secondary loss of a protein band, Huntsman (1970) hypothesized that C. cyprinus was the most "advanced" member of the genus. C. carpio was suggested to be the closest to ancestral ictiobine stock. Based strictly on the results of this study, the sizes at stages of larval development are more similar between C. carpio and C. velifer than they are between either of these and C. cyprinus. However, the description of the development of the quillback carpsucker presented by Gerlach (1973) differs enough from the description produced herein to suggest that geographic and/or genetic factors may produce significant variation in development.

The author is presently pursuing a comparable description of the early development of the genus Ictiobus and the development of a discriminant analysis method for species separation of ictiobine larvae. Other areas of potential research are: the determination of behavioral changes or habitat preference associated with the virtual disappearance of ictiobine larvae from ichthyoplankton at sizes greater than ten millimeters; habitat requirements of ictiobine larvae; food preference of young; and the relationships of larval characters to ontogenetic and environmental factors.

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VITA

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