MORPHOLOGY, PHYLOGENY, BIOGEOGRAPHY AND SYSTEMATICS OF *PHOXINUS* (PISCES: CYPRINIDAE)

by

XING-YU CHEN

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To my mother, father, and Jing,
for their love and encouragement.

CONTENTS

INTRODUCTION

Cyprinidae, the largest freshwater fish family, is divided into two subfamilies (Cavender & Coburn 1992) with 210 genera and 2,010 species (Nelson 1994). *Phoxinus*, belonging to the subfamily Leuciscinae (Chen 1987b, Howes 1991, Cavender & Coburn 1992, Coburn & Cavender 1992), is a small sized genus (less than 100 mm in maximum standard length in most species) with nine species, and is the only minnow genus occurring in both North America and Eurasia. Some species of the genus are widely distributed, others are restricted to small drainage areas. For instance, *P. phoxinus* is widespread in Europe and Asia (Berg 1949, Banarescu 1964), whereas *P. tennesseensis* is found only from the upper Tennessee River drainage of Tennessee and Virginia of USA (Starnes & Jenkins 1988).

Since the type species of *Phoxinus, phoxinus*, was described by Linnaeus in 1758 (as *Cyprinus phoxinus*), hundreds of papers and books related to the genus have been published. Most of the literature is records of geographical distribution, or brief descriptions of the species of the genus. Only a few of these deal with anatomy and phylogenetic relationships of the species in the genus (e.g., Gasowska 1979, Joswiak 1980, Howes 1985). During the last two centuries, the definition of the genus has been an open question, and its content has changed. For instance, *P. neogaeus* has been placed in four different genera (*Phoxinus, Pfrille, Chrosomus*, and *Leuciscus*) since it was described by Cope (1869) (in Günther 1868). A similar situation is also present in other *Phoxinus* species. The unstable taxonomic status of the *Phoxinus* species resulted from lack of a clear definition of the genus, and lack of comprehensive comparisons among *Phoxinus* species and between *Phoxinus* and other related genera. Joswiak (1980) correctly pointed out that this genus "is a focus of controversy involving the relation between Palearctic and Nearctic cyprinids". The situation has not been improved very much since then.

The present study was designed to review the genus *Phoxinus*, and to provide a hypothesis of its relationships with other genera and among its species. This monograph includes seven sections. A historical review of *Phoxinus* is presented first, followed by a phylogenetic analysis among *Phoxinus* and other genera; then I report the results from the comparative morphological study among the species of the genus. Based on the data from these studies, I analyze the phylogenetic relationships among the species of *Phoxinus* and discuss the biogeography of the genus. Then a classification of the genus is followed by an account of the nine recognized species of the genus.

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METHODS

Data Collecting

1. Measurements

Measurements were taken with Dial Calipers reading to 0.1 mm, on the left side of the specimens. Methods for measurements follow Hubbs & Lagler (1947, 1964), except the following which were not defined by those authors:

Prepelvic length is the distance from end of the snout to the base of the left pelvic fin.

Intestine length is the straight length of the intestine. Because the intestine in *Phoxinus* is coiled, it was removed from the body cavity, uncoiled, and then measured.

Length of anterior chamber of gas bladder is the distance between the most anterior point to the most posterior point of the anterior chamber.
Length of posterior chamber of gas bladder is the distance between the most anterior point to the most posterior point of the posterior chamber.
Mouth angle is the angle between the dorsal surface of the head and a plane along the dorsal margin of the lower jaw.

2. Counts

All counts (e.g., branchiostegal rays, fin-rays) were conducted with a Wild Microscope or a Zeiss Microscope. The methods for different counts are described as follows:
Number of rays of paired fins were counted following Hubbs & Lagler (1947, 1964). Number of rays of the dorsal and anal fins consists of procurrent rays (rudimentary unbranched and unsegmented rays) and principal rays of Hubbs & Lagler (1947, 1964). Hereafter the principal rays are referred to "rays". All procurrent rays and rays are counted. Caudal fin-rays were counted as dorsal and ventral procurrent, and dorsal and ventral principal rays.
All lateral line scales were counted. Cephalic lateral line pores were divided into six sections following Reno (1969), except the preoperculomandibular canal which is divided into two sections (mandibular and preopercular sections) in the species of *Phoxinus* (see below). All pores in each section were counted.
Following Chen (1988b) and Chen & Arratia (1994), all primary lamellae were counted as the total number of the primary lamella for each olfactory organ. No secondary lamellae are present on the primary lamellae in *Phoxinus*.
Number of gill rakers on the first gill arch were counted and considered as the number of gill rakers of the specimen.
Number of vertebrae includes all vertebrae (from vertebra 1 to preural vertebra 1, ural centra not included), and are divided into precaudal and caudal ones, according to Mayden (1989). The four vertebrae associated with the Weberian apparatus were counted as four and included in the number of precaudal vertebrae. The count of vertebrae was made on cleared and double stained specimens and some radiographs.

3. Non-osteological and osteological morphology

Non-osteological morphology was studied from 75% alcohol preserved specimens with the microscopes mentioned above. Tubercles and scales were studied also with Scanning Electron Microscope (SEM).

Osteological features were studied on cleared and double stained specimens prepared following Dingerkus & Uhler (1977), and from radiographs of some specimens.

All measurements, counts, and non-osteological data were obtained from more than five specimens for most species studied. In most cases, more than 15 specimens for each species were studied. Whenever possible, more than three specimens of each species were studied in order to collect the osteological data. In most *Phoxinus* species, a series of different sex and size was studied.

The illustrations were prepared using microscopes with camera lucida attachment. The photographs were taken with either camera or SEM.

Terminology

Terms for different parts of the fish body follow Cross (1967), except for a few cases mentioned in the text (e.g., breast scales). Terms for different structures of the olfactory organ follow Chen (1988b) and Chen & Arratia (1994). Terms for different structures of the gas bladder follow Bond (1979).

Phylogenetic analyses

The phylogenetic analyses follow the cladistic methodology (Hennig 1966, Wiley 1981). Polarities of the transformation series were determined by outgroups comparison following Maddison et al. (1984). Ontogenetic data were also used to determine the polarities of a few transformation series though some disadvantages might be present in the ontogenetic criterion in the polarity determinations (Mayden & Wiley 1992).

Because no well-supported hypotheses about the sistergroup of *Phoxinus* are available, the relationship among *Phoxinus* and other closely related minnow genera (grouped as Hemitremians herein) are reevaluated using the Exoglossin Clade of Coburn & Cavender (1992) as the outgroups.

According to the result from the analysis of the relationships among *Phoxinus* and other genera (see below), *Lagowskiella, Rhynchocypris*, and *Eupallasella* were treated as the outgroups for the polarity determination of the transformation series in the phylogenetic analysis among the species of *Phoxinus*. 210 transformation series including non-osteological and osteological characters were analyzed.

The character states (TS) are identified as 0, 1, 2, 3, or 4, among which 0 represents the plesiomorphic state, whereas 1, 2, 3, and 4 correspond to the apomorphic ones. These numbers are present in square brackets following the transformation series number (e.g., TS 100 [0], TS 100 [1]).

PAUP (version 3.0s) (Phylogenetic Analysis Using Parsimony) program (Swofford 1991) was used to generate the phylogenetic hypotheses presented herein for both the Hemitremian Clade and the species of *Phoxinus*.

Abbreviations

A list of abbreviations used in the figures and text is given in appendix IV at the end of the book.

MATERIAL EXAMINED

Forty-seven species of Cyprinidae were studied. The species are grouped as non-*Phoxinus* species and *Phoxinus* species. The non-*Phoxinus* species are mainly used to evaluate the relationships of *Phoxinus* with other genera, and to compare with the species of *Phoxinus*.

The specimens of non-*Phoxinus* species studied are listed below, whereas the specimens of *Phoxinus* are listed in "Species Accounts". The following information and arrangements are provided for specimens of each species of both non-*Phoxinus* and *Phoxinus*: institution acronym and catalogue number, number of alcohol preserved specimens (**alch.**), number of cleared and stained specimens (**C&S**) (if any), the locality collected, the name(s) of collector(s), and the date of collection.

The abbreviations for the institutions follow Leviton et al. (1985), except the following which are not available in the literature:

CNUC	Chonbuk National University, Chonju, Korea
IFFL	Institute of Freshwater Fishery of Liaoning Province, Dalian, China
NAIJ	National Aquacultural Institute, Japan
P	Zoological Museum, the Moscow Lomonsov State University, Russia.

Campostoma anomalum (Rafinesque): KU 3946, 3 C&S, Spring Creek at Big Springs Ranch, Sec 20-21, T325, R28W, Meade County, Kansas, USA; Cross & Nelson; 13 June 1958. – KU 8889, 6 alch.; Catawba River, McDowell County, North Carolina, USA; F.B. Cross et al.; 5 September 1964. – KU 14127, 1 C&S; Long Creek, 1 mi. NW Holland, Allen County, Kentucky, USA; M.E. Braasch et al.; 1 April 1967. – KU 20365, 5 alch.; Blocker Creek, Rt. 84 bridge at Langley, Pike County, Arkansas, USA; R.L. Mayden et al.; 9 April 1982. – KU 20371, 1 alch., Ouachita River, 6 mi. NE Mena on U.S. Rt 71, Polk County, Arkansas, USA; R.L. Mayden et al.; 9 April 1982.

Campostoma ornatum Girard: KU 3251, 15 alch.; Cajon Bonita, 6 mi S U.S. border at Arizona-New Mexico State Line, Sonora, Mexico; S.P. Gordon; March 1954.

Carassius auratus (Linnaeus): KU 8673, 2 alch.; Shellrock River, Worth County, Iowa, USA; E. Beetner et al; 9 August 1964.

Clinostomus elongatus (Kirtland): KU 2751, 5 alch.; Big Creek, 2 mi. north of Chardon, Geauga County, Ohio, USA; J.S. Findley; 11 July 1943. – KU 3881, 2 alch.; Cuyahoga County, Ohio, USA; J. Findley & W.B. Quay; 19 September 1944. – KU 11322, 2 alch. and 2 C&S; Monroe Twp., Machochee Creek, Logan County, Ohio, USA; W.L. Pflieger et al.; 26 April 1958. – KU 21401, 15 alch.; Indian Creek, JCT Ohio Rt 84 and Depot Road, Ashtabula County, Ohio, USA; T. Rosseger & M. Coburn; 5 March 1986.

Clinostomus funduloides Girard: KU 3262, 38 alch. and 2 C&S; N. Fork Roanoke River at Route 11 bridge, Montgomery County, Roanoke County line, Virginia, USA; B. Stough, T. Riggin & W.S. Davis; 17 May 1952. – KU 10697, 4 C&S; Carner's Creek, 9 mi. SW Dickson on Tennessee Rt 48, Tennessee, USA; M.E. Braasch; 20 November 1965. – KU 11424, 45 alch.; Stream near Neuse at Camp Durant, Wake County, North Carolina, USA; W.A. Reid; 17 June 1964. – KU 12065, 5 alch.; Blue Spring Creek, 1 mi. W. Hillsboro, on gravel road S. of US 41, Coffee County, Tennessee, USA; M.E. Braasch; 13 August 1966. – KU 20915, 7 alch.; Whites Creek, 4 mi. North Bath Springs, Decatur County, Tennessee, USA; M.E. Braasch; 4 April 1978. – KU 22253, 33 alch.; Craig Creek at Va. Rt 621, Montgomery County, Virginia, USA; B.K. Wagner et al.; 9 September 1987. – KU 22268, 9 alch.; Craig Creek at VA Rt 621 bridge, Montgomery County, Virginia, USA; B.K. Wagner et al.; 9 September 1987. – KU 22317, 3 alch.; Ararat River at Rt 739 bridge near North Corolina border, Virginia, USA; B.K. Wagner et al.; 13 September 1987.

Couesius plumbeus (Agassiz): KU 18872, 15 alch.; Pine River, Nigger Creek, Michigan, USA; collector unknown; 1 August 1951. – KU 18881, 8 C&S; Poplar River, 9 mi. S Rockglen, Saskatchewan, Canada; G. Gruchy & T.A. Willock; 7 July 1970. – KU 18965, 15 alch.; Box Elder Creek, South Canyon, Pennington County, South Dakota, USA; Dilger, Robins & Hilton; 30 June 1989.

Ctenopharyngodon idella (Cuvier & Valenciennes): KU 21097, 2 alch.; Butler County, Kansas, USA; bait dealer for K. Brunson; 1984.

Cyprinella callisema (Jordan): KU 8842, 11 C&S; Ogeechee River below mill dam at Mayfield, Hancock-Warren County, Georgia, USA; F.B. Cross et al.; 30 August 1964.

Cyprinella nivea (Cope): KU 18987, 6 C&S; Savanah drainage, SFK Broad River, 1.6 mi. S. Rt 72 in Carlton, Maclison County, Georgia, USA; Denoncourt & Wallace; 15 August 1967.

Cyprinella whipplei Girard: KU 14211, 12 C&S; Elk Creek, SW Tahlequah on Oklahoma Rt 82, Cherokee County, Oklahoma, USA; Cross, Collins & Cavin; 22 April 1970.

Cyprinus carpio Linnaeus: KU 1626, 1 dry skeleton, Douglas County, Kansas, USA. – KU 3739, 1 C&S, Churchill Co., NV, USA. – KU 12440, 1 C&S, Elko Co., NV, USA. – KU 22583, 43 alch.; Walnut Creek at diversion dam, Barton County, Kansas, USA; F.B. Cross et al.; 5 June 1986.

Dionda episcopa Girard: KU 7427, 5 C&S; La Augustura Canal, Coahuila, Mexico; W. Minckley; 18 April 1963. – KU 16891, 5 C&S; Pecos River, 4 mi. S. Pandale, Val Verde County, Texas, USA; B. Stewart et al.; 1 November 1975.

Eupallasella percnurus Pallas: AMNH 10926, 5 alch.; Mai-taichao, Shanxi Province, China; Third Asiatic Expedition, C.H. Pope; late April to July 1922. – MCZ 32369, 3 alch.; Vladivostok, Sedanka River, USSR, Asia; Vlad. Fish. Res. Sta.; date unknown. – NMC 77-0889, 4 alch.; Lake in the infra current of the Tugur River (Basin of Okhotsk Sea), USSR; A.R. Kuznetzou; 25 March 1936. – NMC 73-196, 10 alch.; Pond in Rynarzewo near Bydgoszoz, Poland; J.M. Rembiszewskii; date unknown. – USNM 105156, 1 alch.; Middle Amur near Kasatkino, Siberia, Russia; collector unknown; 13 August 1935. – ZIL uncat., 4 alch. and 1 C&S; Lake Khangal, upper Onco, Amur basin, Mongolia; collector and date unknown. – ZIL uncat., 2 alch.; Kolyma River, Russia; collector and date unknown.

Exoglossum laurae (Hubbs): KU 18923, 5 C&S; Little River at National Forest Rt 44 bridge, Pocohantas County, West Virginia, USA; S.A. Pistolis; 11 June 1977.

Exoglossum maxillingua (Lesueur): KU 18924, 10 alch.; Danning Creek at mouth along County Rt. 5042, Bedford County, Pennsylvania, USA; C.H. Hocutt et al.; 19 August 1978.

Gila atraria (Girard): KU 11922, 1 C&S; Park Canyon Creek, 0.3 mi below Lake Enterprise Dam, Washington County, Utah, USA; G. R. Smith; 11 June 1966.

Gila copei (Jordan & Gilbert): KU 11819, 1 C&S; Mammoth Creek above confluence with Sevier River, Garfield County, Utah, USA; Smith & Koehn; 16 April 1966.– KU 11830, 22 alch.; Tributary to Yellow Creek above confluence, T2N, R9E, S4, Summit County, Utah, USA; G.R. Smith & B. Deardon; 24 April 1966.

Hemitremia flammea (Jordan & Gilbert): KU 12066, 1 C&S; Blue spring Creek, 1 mi. W. Hillsboro on gravel road S of US 41, Coffing County, Tennessee, USA; M.E. Braasch; 13 August 1966. – KU 18884, 20 alch.; Dry Branch tributary to Little Cypress Creek, Sec. 4, T15, R11W, Lauderdale County, Alabama, USA; B.R. Wall et al.; 22 March 1969. – KU 18931, 6 alch. and 14 C&S; Crumpton Creek, South of Manchester, Coffee County, Tennessee, USA; Tennessee Valley Authority; 3 October 1972. – KU 20936, 24 alch.; Carrol Creek, 1.5 mi. N. Tullahoma, Coffee County, Tennessee, USA; M.E. Braasch & D. Greaney; 21 April 1988.

Hybognathus hankinsoni Hubbs: KU 2014, 2 C&S; Manganese Lake, Keweenaw County, Michigan, USA; J.M. Lowe; 31 July 1926.

Hybognathus hayi Jordan: KU 9613, 4 C&S; ditch 4 mi. NW Qulin, Sec. 11, T23N, R7E, Butler County, Missouri, USA; W.L. Pflieger et al.; 17 July 1964.

Hybognathus placitus Girard: KU 2020, 24 alch.; North Canadian River, 4 mi. S of Gate, S. 29T4NR28E, Beaver County, Okla, USA; A.B. Leonard; 4 September 1921. – KU 9628, 33 alch.;

Missouri River at Gasconade, T46N, R6W, S5, Gasconade County, Missouri, USA; W.L. Pflieger & party; 26 June 1963. – KU 12597, 3 C&S; Republican River, at Kansas route 148 bridge, 1 mi. W. Norway, Republic County, Kansas, USA; M.E. Braasch; 26 November 1966.

Lagowskiella czekanowskii Dybowski – NMC 77-0884, 5 alch.; small river, Wilyuy district, Eastern Siberia, Knig-Uryah, USSR; Merculov; 20 February 1912.

Lagowskiella lagowskii Dybowski: ANSP 64214, 1 alch.; China; Third Asiatic Expedition; Hsing Lung Shan & E. Tombs; 7 August 1921. – NAIJ 14402-14403, 2 alch. and 2 C&S; Kansong-up, Kosong-gun, Kangwon-do, Pref.; collector unknown; 1 January 1989. – MCZ 3007, 2 alch.; Lake Baikal, Siberia, Russia; J.D.E. Schmeltz, Jr.; 1873. – MCZ 32370, 7 alch.; Chilka River, USSR, Asia; Vlad. Fish. Res. Sta.; 29 April 1929. – USNM 82296-82301, 6 alch.; Hsin Lung Shan District Imperial Hunting Grounds, Northern China, China; A. Sowerby; August 1917. – USNM 179862; 3 alch.; Amur River, Russia; collector and date unknown. – ZIL 15612, 2 alch.; Lake Beloje (Amur River system); collector and date unknown.

Leuciscus leuciscus (Dybowski): KU 10227, 1 C&S; Siberia, Irkutsk; J.F. Aboot; date unknown.

Macrhybopsis aestivalis (Girard): KU 12103, 5 C&S; Kansas River at Dam in Lawrence, Douglas County, Kansas, USA; G.R. Smith & M.E. Braasch; 9 September 1966.

Margariscus margarita (Cope): KU 1139, 5 alch.; Pond in Wilderness Park, Emmet County, Michigan, USA; U.B.S. Ichthyology class; 24 July 1946. – KU 2393, 1 alch.; Big Stone Bay, Michigan, USA; C. Creaser; 26 August 1938. – KU 3556, 1 alch.; Trant River below Trant Lake on HW 51, 9 mi. SW Boulder JCT, Vilas County, Wisconsin, USA; D. Lang; 1954. – KU 8696, 4 alch.; Isabella River at park area, Sec. 36, T60N, R9W, Lake County, Minnesota, USA; E.G. Beetner & C.E. Judd; 13 August 1964. – KU 8519, 11 alch.; Snake River, Cherry County, Nebraska, USA; R. Peckham; 21 August 1963. – KU 16971, 6 alch.; Kenora, Canada Experimental Lakes Area, Lake 226, Ontario, Canada; D. Kettle & D. Wright; 15 October 1976. – KU 19000, 5 alch. and 7 C&S; Oil Creek, 3/4 mi. S. Rawson, Allegheny County, New York, USA; M.A. Hall & E. C. Raney; 26 July 1937. – KU 21501, 4 alch.; Snake Creek, Sec. 36, T31N, R19E, Blain County, Montana, USA; D. Wannamaker; 16 September 1986.

Nocomis biguttatus (Kirtland): KU 12497, 2 C&S; North Fork White River, Sec. 7, T27N, R11W, Douglas County, Missouri, USA; G.R. Smith; 24 May 1967.

Nocomis leptocephalus (Girard): KU 12740, 1 C&S; Buttahatchie River, 12 mi. E. Hamilton, Marion County, Alabama, USA; collector unknown; 8 September 1964.

Nocomis micropogon (Cope): KU 12018, 7 alch.; Dadd's Creek; Catoosa Wildlife Management area, Cumberland County, Tennessee, USA; M.E. Braasch & A. Gnilka; 12 August 1966.

Nocomis platyrhynchus Lachner & Jenkins: KU 18926, 9 C&S; above Wolf Creek on Green Briar river, Summer County, West Virginia, USA; C.H. Hocutt et al.; 29 August 1974.

Notropis buccatus (Cope): KU 18881, 5 alch.; Poplar River, 9 mi. S. Rockglen, Saskatchewan, Canada; C.G. Gruchy & T.A. Willock, USA; 7 July 1970. – KU 22331, 12 alch.; Taylor Branch at Kentucky Rt 478 bridge, McCreary County, Kentucky, USA; B.K. Wagner et al.; 5 March 1988.

Opsariichthys uncirostris Günther: KU 21448, 1 alch.; Hanjian River, China; collector and date unknown. – KU 21949, 1 alch. and 1 C&S; Lake Biwa, Japan; collector unknown; 1 March 1941.

Platygobio gracilis (Richardson): KU 11950, 1 C&S; Jemez River at Jemez, Sandoval County, New Mexico, USA; R.K. Koehn et al.; 27 July 1966. – KU 17257, 6 alch.; Moreau River between Whitehorse and Promise, Dewey County, South Dakota, USA; H.A. Martyn & D. Schooley; 11 October 1974.

Rhynchocypris oxycephalus Mori: CNUC uncat., 4 alch. and 2 C&S; Namgo-dong, Chonju-S, Chollabuk-do, Pref., Korea; collector unknown; 2 April 1988. – FRLM 10769, 1 alch.; Hozumi-cho, Gifu Pref., Japan; collector unknown; 14 April 1990. – FRLM 10776, 1 alch.; Hozumi-cho, Gifu Pref., Japan; collector unknown; 14 April 1990. – FRLM 10777, 1 alch.; Hozumi-cho, Gifu Pref., Japan; collector unknown; 14 April 1990. – FRLM 10890, 1 alch.; Nigori River, Mie Pref., Japan; collector unknown; 4 May 1990. – FRLM 10891, 1 alch.; Nigori River, Mie Pref., Japan; collector unknown; 4 May 1990. – FRLM 10895, 1 alch.; Nigori River, Mie Pref., Japan; collector unknown; 4 May 1990. – FRLM 10896, 1 alch.; Nigori River, Mie Pref., Japan; collector unknown; 4 May 1990. – FRLM 10898, 1 alch.; Nigori River, Mie Pref., Japan; collector unknown; 4 May 1990. – USNM 105116, 1 alch.; (Siberia) Sedanka River near Vladivostok, USSR; collector unknown; 24 September 1929.

Rutilus rutilus Linnaeus: KU 22430, 1 alch. and 2 C&S; Hessen, Germany; T. Martin, USA; August 1988.

Semotilus atromaculatus (Mitchill): KU 12482, 1 C&S; Hog Creek, Highway 63, Crossing South of Houston, Texas County, Missouri, USA; G.R. Smith; 24 May 1967. – KU 12594, 6 C&S; East Fork Clarks River, 1 mi E. Hardin, Marshall County, Kentucky; M.E. Braasch et al.; 4 April 1967. – KU 13197, 2 C&S; Deep Creek, at HW 70 Cross, Wabaunsee County, Kansas; Roy Irwin, USA; 7 June 1966.

Semotilus corporalis (Mitchill): KU 16915, 5 alch.: S Fork of S Branch of Potomac River, between Moorefield and Fisher, Hardy County, West Virginia, USA; N.H. Douglas et al.; 14 April 1971. – KU 18856, 20 alch.; South Fork of South Branch of Potomic River between Moorefield and Fisher, Hardy County, West Virginia, USA; N.H. Douglas et al.; 14 April 1971. – KU 21770, 12 alch.; Back Creek, Bath County, Virginia, USA; S.M. Smith et al.; 29 October 1986. – KU 21817, 23 alch.; Back Creek, Bath County, Virginia, USA; S.M. Smith et al.; 31 October 1986.

Zacco platypus (Schlegel): KU 12320, 2 alch. and 1 C&S; Siquokaken Inasagun Inasa-Machi Jingujigawa River below Misogi Bridge Miyakodagawa River, Japan; Hasegawa Vyeno; 8 July 1964. – KU 12321, 2 alch.; Kusu-gun Kokonoe-Machi Migita, Kusu River (Tributary of Chikugo River), Kyushu, Japan; Villagers; 22 August 1965.

HISTORICAL REVIEW OF *PHOXINUS*

As mentioned in the Introduction, *Phoxinus* is a very interesting group because it is the only minnow genus occurring in North America and Eurasia. Since the first species of *Phoxinus* was described – *Phoxinus phoxinus* (Linnaeus, 1758) – many ichthyologists have been attracted by these fishes to study different aspects of the genus, such as taxonomy, distribution, osteology, behavior, and physiology. Here, I chronologically summarize the literature of the genus, mainly on those related to taxonomy, morphology, and distribution. For sake of convenience, I treat every 10 years as an artificial unit except the parts "up to the 20th century", including the publications before 1900, and "1980-1994" consisting of a summary of 15 years' publications.

Up to the 20th century

The first species of *Phoxinus* was described by Linnaeus in his **Systema Naturae** (10th ed., 1758) as *Cyprinus phoxinus*. As for other species described by Linnaeus (1758), the description of this species was very brief. Another species described by Linnaeus (1758), *Cyprinus aphya*, is generally considered a synonym of *Phoxinus phoxinus* (e.g., Berg 1949, Banarescu 1964, Wheeler 1991).

Rafinesque, one of the most important naturalists in the 19th century, considered the genus *Cyprinus* of Linnaeus beeing too diverse and thus split it into several genera based on "the position of the dorsal fin and the vent, the number of rays to the abdominal fins" (Rafinesque 1820a, b, 1889). Among these genera, three occur in Europe and one (*Minnilus*) in North America (Rafinesque 1820a, b, 1899).[1] *Phoxinus*, a European genus, differs from the other two European ones, *Dobula* and *Alburnus*[2], in "ten abdominal rays and no appendage" (Rafinesque 1820a, 1889).

In the same papers, Rafinesque (1820a, b, 1889) described the subgenus *Chrosomus* of *Luxilus* for the "redbelly shiner" from Ohio River, and named the shiner as *Luxilus erythrogaster*. However, Rafinesque also suggested that the subgenus *Chrosomus* might also be considered as a genus. Therefore, the name for this "redbelly shiner" was often cited as *Chrosomus erythrogaster* (Rafinesque) (e.g., Cross 1967) or *Chrosomus erythrogaster* Rafinesque (e.g., Eddy & Underhill 1974). [Both are synonyms of *Phoxinus erythrogaster* (Rafinesque), see below]. This might be an explanation why both *C. erythrogaster* (Rafinesque) and *C. erythrogaster* Rafinesque appear in the literature (cf. species account of *Phoxinus erythrogaster*), though the correct citation should be *Chrosomus erythrogaster* (Rafinesque), not *C. erythrogaster* Rafinesque.

A more complicated and confusing problem was raised by the dates of the publications of Rafinesque (1820a, b; 1889). All of the literature known cited Rafinesque 1820b:45 as the original description of *Phoxinus* Rafinesque, Rafinesque 1820b:47 as the original description of *Chrosomus*, and Rafinesque 1820b:47 as the original description of *Chrosomus erythrogaster* (Rafinesque) (e.g., Starnes & Starnes 1980a, Howes 1985). However, according to the zoological nomenclature rules, the correct citation should be the one published first. Rafinesque's paper on the fishes of Ohio River, in which *Phoxinus, Chrosomus*, and *Chrosomus erythrogaster* were originally described, was published three times under two different titles (i.e., Rafinesque 1820a, b, 1889). Rafinesque (1820a) was published in the journal "The Western Review and Miscellaneous Magazine, a monthly publication" as one of a series of nine papers under the title "Fishes of the River Ohio" published from December 1819 to December 1820 (Eschmeyer 1990). (This magazine was published in Lexington, Kentucky, only from 1818 to 1820.) The paper originally describing *Phoxinus, Chrosomus*, and *Chrosomus erythrogaster* (Rafinesque 1820a) was the fourth in the series and was published in May 1820. Rafinesque (1820b) was published on 22 May 1820, as a separate monograph titled "Ichthyologia Ohiensis, or natural history of the fishes inhabiting the River Ohio and its tributary streams, preceded by a physical description of the Ohio and its branches." The contents of Rafinesque's papers (1820a, b) are the same. Rafinesque (1889) consists of 250 copies reprinted from Rafinesque (1820b). We do not have any evidence to show whether Rafinesque (1820b) was published earlier than Rafinesque (1820a) because there is no date for Rafinesque (1820a).

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[1]) *Minnilus*, a synonym of *Notropis* (Eschmeyer 1990: 248), was misspelled as *Minulus* Rafinesque, 1820a:236 and *Minnulus* Rafinesque, 1820a:237.

[2]) *Alburnus* Catesby, 1771 in Sciaenidae is not an available name because it was published in a rejected work (Eschmeyer 1990:18).

It is possible that the serial papers (at least some of them) were published first, then followed by Rafinesque (1820b) as a collection of these serial papers. (Eschmeyer 1990:605 cited the date of Rafinesque 1820b as December 1820.) If the above argumentation is accepted, we then should cite "Rafinesque 1820a" as the original description of *Phoxinus, Chrosomus*, and *Chrosomus erythrogaster*, instead of "Rafinesque 1820b." Based on the above discussion, I therefore cite Rafinesque (1820a) as the original description of *Phoxinus, Luxilus erythrogaster*, and *Chrosomus erythrogaster*.

Using *Cyprinus phoxinus* Linnaeus as the type species (as Rafinesque 1820a did), Agassiz (1835:37) established a genus *Phoxinus* for *Cyprinus phoxinus*, and assigned *Cyprinus phoxinus* as *Phoxinus laeves*.

Jordan (1916) demonstrated that the name of the genus *Phoxinus* should be *Phoxinus* Rafinesque, 1820, not *Phoxinus* Agassiz, 1835, because Rafinesque (1820a) was published earlier than Agassiz (1835). Unfortunately, Jordan's papers did not soon get the attention of the active ichthyologists. Many recent publications still cited *Phoxinus* Agassiz as the valid name (e.g., Berg 1949, Yang & Hung 1964, Smith 1979, Heese 1981) without discussion. However, from the above discussion, it is clear that *Phoxinus* Agassiz, 1835 is a synonym of *Phoxinus* Rafinesque, 1820a.

Cope (1862) described another *Chrosomus* species, *C. eos*, from Meshoppen Creek in Susquehanna County of Pennsylvania, USA. He compared *C. eos* with *C. erythrogaster* and indicated as differences between *C. eos* and *C. erythrogaster* the presence or absence of the lateral line and the body shape. Two years later, Cope (1864) compared the two species and found some of the *C. eos* specimens exhibiting a short lateral line, whereas others entirely lacked pored scales. Though Cope (1869) considered the specimens of *C. eos* in Cope (1864) as *Phoxinus neogaeus*, some of these specimens might be indeed *C. eos* because in some specimens the lateral line "is wanting" (Cope 1864). In *P. neogaeus*, there is a short lateral line (Cope 1869). It is necessary to notice that intraspecific variation of the lateral line is present in the species of *Phoxinus*.

Phoxinus neogaeus was described by Cope (1869) from New Hudson, Livingston County, Michigan, in "Synopsis of the Cyprinidae of Pennsylvania." Cope (1869) was the first one to allocate North American species to the European genus *Phoxinus*. He (Cope 1869) distinguished *P. neogaeus* from *P. laevis* (i.e., *P. phoxinus*) by "its scaly vertebral and ventral region, and much shorter lateral line." Three *Phoxinus* species were reported from Pennsylvania (i.e., *P. neogaeus, erythrogaster*, and *eos*) (Cope 1869).

The proper date and source for the original description of *Phoxinus neogaeus* is problematic. Cope's paper describing *P. neogaeus* was published in 1869 (Cope 1869). However, it was cited, with a description of the species, by Günther (1868). The date 1869 was widely cited in literature until Gilbert (1971). This confusion might be partially due to the failure of ichthyologists to check the literature thoroughly (Gilbert 1971). The correct date for this species should be cited as *Phoxinus neogaeus* Cope, 1868, as suggested by Robins et al. (1991).

Günther (1868) did not believe *Phoxinus* to be present in Europe, but only in North America, and considered *P. phoxinus* as *Leuciscus phoxinus*. He divided the two North American *Phoxinus* species into two categories: *P. neogaeus* with two rows of pharyngeal teeth, and *erythrogaster* with one row of pharyngeal teeth, but both bearing an incomplete body lateral line.

The fourth North American *Phoxinus* species, *P. oreas*, was described by Cope (1868) from Roanoke of Montgomery County, Virginia, as *Chrosomus oreas*. This species resembles *Phoxinus eos* (Cope 1868); the most obvious difference is in their coloration pattern (Cope 1868).

Jordan (1885) recognized two species under the genus *Chrosomus*: *C. erythrogaster* and *C. oreas*, and stated *C. eos* identical to *C. erythrogaster*. In the same publication, Jordan recognized 20 species under *Phoxinus* from North America which he split into six subgenera: *Clinostomus, Tigoma, Siboma, Squalius, Cheonda*, and *Phoxinus*. Most of these subgenera were raised to genera by Jordan (1924).

Jordan & Evermann (1896), in their four volumes of "The Fishes of North and Middle America", considered *Phoxinus* as one of the eight subgenera included in *Leuciscus*. Three species were assigned under the subgenus *Phoxinus: P. neogaeus, margarita*, and *orcutti*. They listed three species under *Chrosomus* and pointed out that *Chrosomus* showed many similarities with *Phoxinus* although none of the similarities were listed.

As in other fish groups, research on *Phoxinus* during these years focused mainly on the description of new species and new records of geographical distribution. Detail morphological study was not yet conducted.

1900-1919

Smith (1908) studied the social spawning behavior of *Phoxinus erythrogaster*. This was the first behavioral account of *Phoxinus* species. He also described the morphology of the pearl organ (breeding tubercles) though the author did not recognize the breast tubercles of the breeding males. Sexual dimorphism between the male and female of *P. erythrogaster* was shown by body color, relative size of pectoral fin, and "pearl organs" (Smith 1908).

Cockerell & Callaway (1909) studied the scale morphology of some North American cyprinids and separated the subfamily Chondrostominae of Jordan & Evermann (1896) into four subfamilies. *Chrosomus* was assigned in the subfamily Chrosominae. Cockerell & Callaway (1909) considered *Chrosomus* a very primitive group which "might be an ancient offshoot from the stem which gave rise to Cyprinidae and Catostomidae."

Cockerell (1909) reviewed the nomenclature of North American fishes called *"Leuciscus"* and *"Rutilus"*. He demonstrated that the European *"Leuciscus"* and *"Rutilus"* differ from the so-called *"Leuciscus"*- and *"Rutilus"*-species in North America. Cockerell also studied the scales of *Phoxinus* and *Chrosomus*, and pointed out that the scales of both genera were of the same type, minute with radii in all fields. This was the first time that the similarity between European *Phoxinus* and the North American *Chrosomus* was pointed out. (Jordan & Evermann 1896 noticed the two "genera" were similar, but they did not state what was the similarity the "genera" shared. See the above discussion.)

Following Cockerell (1909), Jordan (1916) demonstrated there was no true "*Leuciscus*" in North America and pointed out that the subgenus *Phoxinus* of *Leuciscus* needed to be raised to generic level. However, Fowler (1918) disagreed with Cockerell (1909) and Jordan (1916). Fowler (1918) studied the cotype of *P. neogaeus* Cope (ANSP 4548) and believed there were *Leuciscus* species in North America. As the result, Fowler (1918) considered *P. neogaeus* Cope as *Leuciscus neogaeus*.

1920-1929

Based mainly on the type material of some cyprinids studied by Baird, Girard and Cope, Fowler (1924) studied the North American cyprinids, and assigned *Chrosomus* with two species, *C. erythrogaster* and *C. oreas*, as a genus of the subfamily Chrodrostominae.

Jordan (1924) reviewed the North American dace allied to *Leuciscus* and proposed a new genus *Pfrille* for *Phoxinus neogaeus* Cope. In the footnotes, Jordan (1924:71) indicated *Pfrille* closely related to *Phoxinus*. *Pfrille* was accepted as a valid genus name until Bailey (1951) considered *Pfrille* a synonym of *Chrosomus*. However, *Pfrille* was used later by some authors (e.g., Stasiak 1972).

Jordan & Hubbs (1925) studied fishes from Japan and proposed a new genus, *Moroco*, based on *Pseudaspius bergi* Jordan & Metz, 1913 as type species. However, *Moroco* was considered a synonym of *Phoxinus* by Berg (1932, 1949) and Banarescu (1964), because *Pseudaspius bergi* was considered a synonym of *Phoxinus lagowskii variegatus* (Berg, 1932), or of *P. lagowskii oxycephalus* (Berg, 1949). (*P. lagowskii variegatus* is a synonym of *P. lagowskii oxycephalus* in Berg 1949.) The synonymy in Berg (1932, 1949) was challenged by several ichthyologists (e.g., Okada 1960, Banarescu 1964, Gasowska 1979). Gaswoska (1979) considered *Moroco* a valid genus name, and three species, *Moroco percnurus* (= *P. percnurus* of Berg 1949), *M. lagowskii oxycephalus* (= *P. lagowskii oxycephalus* of Berg 1949), and *M. czekanowskii* (= *P. czekanowskii* of Berg 1949), were included in the genus. Howes (1985) considered *Moroco* a junior synonym of *Lagowskiella*.

Fishes from Ontario of Canada were studied by Hubbs & Brown (1929). Two species of *Phoxinus neogaeus* and *P. erythrogaster* were reported. Hubbs & Brown (1929) noticed the specific breast tuberculation of breeding males of these two species and *P. oreas*. Based on this character, Hubbs & Brown (1929) claimed that these three species share a close relationship. This was the first time that the breast tuberculation of the breeding males was observed in *Phoxinus*.

1930-1939

Berg (1932) published a book on the freshwater fish fauna in Russia, and prepared a synonym list of *Phoxinus*. The list includes *Rhynchocypris* Günther, 1889, *Eulinneella* Dybowski, 1916, *Czekanowskiella* Dybowski, 1916, ?*Pfrille* Jordan, 1924, and *Moroco* Jordan & Hubbs, 1925.

The life history of *Clinostomus elongatus* was studied by Koster (1939), who noticed a roughly triangular patch of scales with one to several more or less developed tubercles on each scale present on the breast of this species. Based on the character of this tuberculation and the color pattern, Koster (1939) proposed a close relationship between the *Chrosomus-Pfrille* group and *Margariscus-Clinostomus-Couesius lumbeus* group.

Bullough (1939, 1940) studied the reproductive cycle of *P. phoxinus*. An internal reproductive rhythm able to work without the external seasonal change was reported (Bullough 1939).

1940-1949

During these years, a few studies on the biology of species of *Phoxinus* were conducted. Frost (1943) studied the natural history of *P. phoxinus*, such as habits, age, growth, food, and reproduction. Frost (1946) also demonstrated dietary relationships among *P. phoxinus* and its associated fish species. The lateral line of *P. phoxinus* was studied by Lekander (1949).

Berg (1949) (1964, English translation) reviewed the Eurasian *Phoxinus* species and proposed a synonym list of the genus. This synonymy, in fact, is a modification of that in Berg (1932). The difference between these two synonymies is that *Gila* Baird & Girard of North America was added to the synonymy of Berg (1932) in Berg (1949), as a subgenus of *Phoxinus*. A key was provided for the eight Eurasian species in Berg (1949). However, *Gila* was removed from *Phoxinus*, and considered as a valid genus name by Uyeno (1960).

1950-1959

Bailey (1951) first lumped *Pfrille* into *Chrosomus* though this lumping was challenged by a few ichthyologists (e.g., Gasowska 1979). Underhill (1957) studied the relationships between the distribution of minnows and darters and Pleistocene glaciation in Minnesota, USA. Three species of *Phoxinus* including *P. neogaeus, eos*, and *erythrogaster* were found in Minnesota. These species, based on Underhill (1957), had three different origins in Minnesota. *P. eos*, which was common in the state, might have arrived at the earliest time. *P. erythrogaster* was considered as a late migrant from the lower Mississippi basin, and ecologically restricted in the region. *P. neogaeus*, common in Lake Superior and the Hudson Bay drainage system but absent or represented by relicts in other basins, did not enter from the Lower Mississippi basin (Underhill 1957).

1960-1969

Bailey & Allum (1962) suggested that populations of two species of *Phoxinus neogaeus* and *P. eos* in South Dakota are glacial relicts. These authors also found that hybrids of *P. neogaeus x P. eos* were common.

Banarescu (1964) reviewed the synonyms of *Phoxinus*. Though I can not agree with some of his synonyms, Banarescu (1964) is one of the most important works in the systematics of *Phoxinus*. At least two contributions to the taxonomic study of the genus were made by Banarescu (1964). He is the first one to consider the North American *Chrosomus* Rafinesque a synonym of *Phoxinus*; he also confirms *Pfrille* Jordan a synonym of *Phoxinus*. The differences between the synonymies of Banarescu (1964) and Berg (1949) are two: (1) Banarescu considered *Chrosomus* Rafinesque as a synonym of *Phoxinus*; and (2) Banarescu deleted *Gila, Eulinneella, Lagowskiella, Eupallasella*, and *Czekanowskiella* from the synonym list of Berg (1949). Banarescu's synonymy, especially his opinion on

Chrosomus as a synonym of *Phoxinus*, was soon accepted by many North American ichthyologists (e.g., Bailey et al. 1970, Mahy 1979c). Under *Phoxinus*, 14 species were listed and a distribution map was provided for *P. phoxinus* (Banarescu 1964).

Starmach (1963) studied the morphological characteristics of *P. phoxinus* from the basin of the Mszanka Stream, Poland. No gender difference among different portions of the body was found for *P. phoxinus*. However, the pharyngeal tooth formulae varied greatly among individuals, even in the same population, as noted by Berinkey (1968). Six different combinations (i.e., 1,4-4,0, 1,4-4,1, 1,4-4,2, 2,4-4,1, 2,4-4,2, and 2,5-4,2) were observed in a small population (17 specimens) from Montenegro, Yugoslawia (Berinkey 1968). It is interesting that the widely used tooth formula, i.e., 2,5-4,2, for *P. phoxinus* presents only a small portion (6%) of the 17 specimens studied by Berinkey (1968).

Yang & Huang (1964) considered *Phoxinus* Aggasiz a valid name and described seven species in the genus from China. A key was provided for the seven species of *Phoxinus*. This was the most comprehensive review of Chinese *Phoxinus* at that time. However, no synonymy of *Phoxinus* was provided by Yang & Huang (1964).

Hill & Jensen (1968) studied numbers of fin rays (pectoral, dorsal, and anal fins) of *Phoxinus erythrogaster* from Big Spring, Johnson County of Oklahoma, USA. They found that variation of the number of rays in the pectoral fin was ontogenetically significant, whereas the number of dorsal and anal fin-rays did not change much in different age groups. They therefore concluded that the number of dorsal and anal fin-rays were less variable than the pectoral fin rays, thus the former two were more useful as taxonomic characters.

Phillips (1968a) studied 24 morphological characters of *Phoxinus erythrogaster* and *eos*. No geographic variation in either species was found. The distribution of the two species in Minnesota was also discussed in Phillips (1968a). Phillips (1969a) compared the morphology of *P. erythrogaster* and *eos* and their geographic variation in Minnesota. The only differences between the two species are the mouth angle and the ratio of snout length to postorbital length. Joswiak & Moore (1982) reanalyzed Phillips' (1969a) data and indicated the two species be distinguishable by these characters.

Besides the taxomonic studies, data on biology of *Phoxinus* were also accumulated in these years. Tyler (1966) studied the lethal temperature of *P. eos* and *neogaeus* in Ontario, Canada. Phillips (1969b) studied the diet of *P. erythrogaster* in Minnesota, USA. Phillips (1969c) also reported the fecundity of *P. erythrogaster*. Hybrids within *Phoxinus* and between *Phoxinus* and other minnows were described, such as *P. eos x P. neogaeus* (New 1962), *P. erythrogaster x Notropis cornutus frontalis, P. erythrogaster x Semotilus atromaculatus* (Cross & Minckley 1960), *P. erythrogaster x Notropis cornutus*, and *P. erythrogaster x Dionda nubila* (Phillips & Etnier 1969).

1970-1979

Although some authors considered *Margariscus margarita* belonging to the same genus as that *Phoxinus neogaeus* was assigned to (e.g., *Leuciscus* in Günther 1868; *Phoxinus* in Jordan 1885), most ichthyologists placed *Margariscus margarita* and *P. neogaeus* in different genera. By studying the hybrids of *Semotilus margarita* (= *Margariscus margari-*

ta) with other *Phoxinus* species (*P. eos* and *P. neogaeus*) and the chromosome number (2N=50), Legendre (1970b) proposed changing the name of this species (*S. margarita*) to *Phoxinus margarita*. However, no other ichthyologists have followed this suggestion.

Stasiak (1972) studied the morphology and life history of *Phoxinus neogaeus*. He supported *Pfrille* as a valid genus for *neogaeus*. However, in a later study Stasiak (1977) changed *Pfrille neogaea* to *Chrosomus neogaeus*.

Mahy (1972) briefly reported his results from an osteological comparison between North American *Phoxinus* species and *P. phoxinus*. Following this, in three serial papers, Mahy (1975a, b, c) studied the osteology of *P. neogaeus, erythrogaster*, and *oreas*. It is worthwhile to note that Mahy used the name *Chrosomus neogaeus* in one (Mahy 1975a), and *Phoxinus neogaeus* in the others (Mahy 1975b, c). Mahy (1975c) recognized two groups of nearctic *Phoxinus* species, *P. neogaeus* group and *P. erythrogaster* group. The first group, including one species, *P. neogaeus*, was the closest to *P. phoxinus*. The second group included the rest of the nearctic *Phoxinus* species known by then. Mahy lumped all species of the second group into a single species, *P. erythrogaster*, i.e., all the nearctic *Phoxinus* species (except *P. neogaeus*) were considered different subspecies of *P. erythrogaster*. Thus, three subspecies were proposed in *P. erythrogaster*, i.e., *P. erythrogaster erythrogaster, erythrogaster oreas*, and *erythrogaster eos* in North America (Mahy 1975c). However, Mahy's "subspecies view" has not been accepted by other ichthyologists.

Gasowska (1979) accepted neither Banarescu's (1964) synonym list nor Mahy's "subspecies" view. Having studied the osteological characters, Gasowska (1979) considered *Moroco* and *Pfrille* as valid generic names. Gasowska (1979) separated the North American *Phoxinus* species into three groups belonging to different taxonomic levels and considered shape of the pharyngeal process of the pharyngeal bone as the main character to recognize different genera. Gasowska proposed a new genus, *Parchrosomus*, for *Phoxinus oreas* because of the broad pharyngeal process, the shape of the urohyal, and its "lateral head is smaller than the maximal body depth, whereas in the two former species (*P. erythrogaster* and *eos*) the lateral head length is larger than the maximal body depth" (Gasowska 1979). Therefore, according to Gasowska (1979), *P. phoxinus, neogaeus*, and *Chrosomus oreas*, and other North American "*Chrosomus*" species belong to three different genera: *Phoxinus, Parchrosomus*, and *Chrosomus*. However, I have found no publication citing *Parchrosomus* as a valid genus. One of the major problems in Gasowska (1979) is that the author did not recognize the specific breast tuberculation in his "*Chrosomus*" species though he did notice the presence of the tuberculation in *P. phoxinus* and *neogaeus*.

Gosline (1978) proposed four subfamilies for Cyprinidae. Among the subfamilies, Leuciscinae are a very big one including almost all North American minnows and some European cyprinids. According to Gosline (1978), *Phoxinus* is an adaptive form of Leuciscinae.

The fifth North American *Phoxinus* species, *P. cumberlandensis*, was described by Starnes & Starnes (1978) from Kentucky. Starnes & Starnes (1978) proposed two groups of *Phoxinus* species in North America: *P. oreas* group (including *P. oreas* and *cumberlandensis*), and *erythrogaster* group (including *P. eos* and *erythrogaster*) based on the morphology of opercles and intestines, and coloration patterns.

During this period (1970-1979), life history, ecology, and behavior of *Phoxinus phoxinus* attracted many ichthyologists' attention. Wootton & Mills (1979) studied the breeding behavior of *P. phoxinus* in a small lake in Europe. Stott & Buckley (1979) observed *P. phoxinus* avoiding their home range when water was deoxygenated but back home when oxygen was restored. Wootton et al. (1980) studied the relationships between body weight and daily food consumption. Settles & Hoyt (1978) studied the reproductive biology of *P. erythrogaster* from Kentucky.

Some papers describing hybrids were published in these years, such as those by Legendre (1970b) and Stasiak (1972) (*Phoxinus neogaeus x P. eos*), and Greenfield et al. (1973) (*P. erythrogaster x Notropis cornutus*).

1980-1994

Joswiak (1980) studied the karyotype of five known nearctic *Phoxinus* species and *P. phoxinus*. He demonstrated 2N=50 for all studied *Phoxinus* species, and his karyotype data supported the lumping of *Phoxinus* and *Chrosomus*. Based on the Nei distance among the *Phoxinus* species, Joswiak (1980) proposed a phylogenetic tree for *Phoxinus*. The tree shows that *P. eos* and *erythrogaster* were derived from *P. oreas*-like ancestor. Joswiak considered his study an evidence supporting the Bering bridge connection for the migration of *Phoxinus* from Eurasia to North America.

Coad (1984) described some *P. phoxinus* specimens with deformed vertebral columns, and Banbura (1985) reported a case of *P. phoxinus* without pectoral fins.

Leuciscinae is a most problematic subfamily in cyprinids to which *Phoxinus* is generally assigned. A few serial papers on the anatomy and relationships of Leuciscinae were published by Howes (1978, 1984, 1985, 1991), though the monophyly of the subfamily is still an open question. Having studied the anatomy and phylogeny of some Chinese carps (e.g., *Ctenopharyngodon* and *Hypophthalmichthys*), Howes (1984) proposed that at least four monophyletic groups could be recognized within Leuciscinae: aspinine, abramine, alburine (raised to subfamily level in Howes 1991), and phoxine with two genera, *Phoxinus* and *Couesius* (Howes 1985, 1991). Howes (1985) reviewed the synonyms of *Phoxinus* and proposed a new synonym list for the genus. This synonym list is a modification of those in Berg (1949) and Banarescu (1964). According to Howes (1985, 1991), *Phoxinus* and *Couesius* share the comb-like tuberculation on the breast scales in breeding males (Howes 1985) and form a sistergroup[1]. Howes (1985) is an important contribution to the study of *Phoxinus* because this was the first one to review the synonyms of *Phoxinus* systematically.

Kim & Kang (1986) studied the osteology of *Moroco keumgang* from Korea. Based on the comparison between *Moroco* and *Phoxinus*, the authors claimed *Moroco* as the sistergroup of *Phoxinus*. They proposed the following synapomorphies for the two genera: the presence of the anterior myodome, the lower part of the interorbital septum extended

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[1]) However, as discussed below and Chen & Arratia (1996), the breast tuberculation of the two genera shows a great difference.

and contacting the parasphenoid, and a relatively straight parasphenoid (Kim & Kang 1986).

Chen et al. (1984) published a hypothesis of phylogenetic relationships among the major groups of Cyprinidae. They proposed ten subfamilies, among which *Phoxinus* belongs to the subfamily Leuciscinae. The content of the subfamily Leuciscinae of Chen et al. (1984) is similar to that of Gosline (1978). However, Howes (1991) complained that the analysis of Chen et al. (1984) was not a cladistic one, although the authors claimed so. Chen et al. (1984) did not provide synapomorphies to support some sistergroup relationships and some subfamilies are recognized by plesiomorphies only.

Cavender & Coburn (1987) studied the evolutionary relationships among eastern North American cyprinids. They stated that *Phoxinus, Semotilus, Couesius, Hemitremia*, and *Clinostomus* share a unique type of anal fin suspension, and the anterior placement of the anal fin pterygiophores. In a later study of the phylogenetic relationships of cyprinids, Cavender & Coburn (1992) recognized two subfamilies, i.e., Cyprininae and Leuciscinae, in the family Cyprinidae. *Phoxinus* was placed in the phoxinin tribe of Leuciscinae.

Chen (1986a, b, 1987a, b) studied the osteology and phylogeny of Chinese leuciscines. He proposed the Chinese leuciscines a monophyletic group and included *Phoxinus* in the subfamily Leuciscinae.

During the study of fish fauna of Huang He (Yellow River) in China, Chen (1988a) described a new *Phoxinus* species, *P. tchangi* from the Huang He tributary. The olfactory organ of *Phoxinus* was studied by Chen (1988b). Chen (1988b) considered the olfactory organ of *Phoxinus* a primitive condition in Cyprinidae because the types of the olfactory organ in *Phoxinus* were commonly found in Cyprinidae.

The sixth North American *Phoxinus* species, *P. tennesseensis*, was described by Starnes & Jenkins (1988) from the Tennessee River drainage, USA. Starnes & Jenkins (1988) also proposed *P. cumberlandensis* the sister species of *[P. oreas + tennesseensis]*, and *P. eos* the sister species of *P. erythrogaster*.

Banarescu (1989) analyzed the distribution patterns of European freshwater fishes. Two patterns were proposed: vicariant and dispersal. In this paper, Banarescu considered *P. phoxinus* the vicariant sister of *P. neogaeus* though no evidence was discussed (Banarescu 1989).

Bugutskaya (1987, 1988a, b, 1989, 1990, 1991) published several papers on the osteology and classification of Leuciscinae based mainly on the Eurasian genera. She recognized eight tribes in the subfamily: Leuciscini, Alburnini, Phoxini, Abramini, Aspinini, Elopichthyini, Pseudoaspini, and Hypophthalmichthyini.

The external morphology and biology of *P. phoxinus* from River Skawa of Poland were studied by Heese (1981, 1984). He stated the maximum age of *P. phoxinus* to be more than six years. Sexual dimorphism of the species was shown in the shape of pectoral and ventral fins, the coloration, and the tuberculation (Heese 1981, 1984). Heese's result was similar to that of Frost (1943).

Based on field work in Mongolia in 1984, Travers (1989) described the Mongolian fish fauna. *P. phoxinus* was caught from "Arctic and Pacific basins." Travers (1989) demonstrated that this species "appears to prefer cold, clear water running over a sand and stone substrate and was often together with *Nemacheilus, Misgurnus*, and young salmonids."

Reproductive biology of *Phoxinus phoxinus* was studied by Mills (1987). Mills (1987) reported the reproductive size for *P. phoxinus* at 50 mm length. The behavior of *P. phoxinus* was described by some European ichthyologists. Partridge (1980) and Magurran & Girling (1986) studied the schooling of the species. Kennedy (1981) observed the homing tendency of the species. Legkiy & Popoya (1984) demonstrated that one of the important factors for the downstream migration of *P. phoxinus* was a change in their photoreaction (negative response). Pfeiffer et al. (1985) indicated *P. phoxinus* bear alarm cells through the year. Bioenergetic biology of the species was studied by Cui & Wootton (1988a, b, 1989). Distribution and ecology of *P. cumberlandensis* was studied by O'Bara (1990, 1991).

Wheeler (1991) discussed the status of the type specimens of *P. phoxinus*. The specimens were in very poor condition and Wheeler was not able to identify whether the specimens were the type of the species (see the discussion in the species account of *P. phoxinus*), thus a problem was raised if the specimen is the "real" type of *P. phoxinus*.

Summary

Since the description of *Cyprinus phoxinus* was published (Linnaeus 1758), almost 240 years have passed. In the past more than 200 years, ichthyologists have paid much attention to the genus *Phoxinus*, publishing hundreds of studies related to these fishes. The main contributions during these years can be summarized as follows:

1. Numerous records of the geographic distribution of the genus;
2. Accumulation of data on life history, ecology and behavior of some species, such as *P. phoxinus* and *erythrogaster*;
3. Some knowledge of osteology and external morphology of some species; and
4. Synonyms of some species.

PHYLOGENETIC RELATIONSHIPS OF *PHOXINUS* AND THE RELATED GENERA

Monophyly of the Hemitremian clade and its position in the family Cyprinidae

According to Chen et al. (1984) and Cavender & Coburn (1992), Cyprinidae comprises two major lineages, the subfamilies Cyprininae and Leuciscinae (Cavender & Coburn 1992) (Fig.1). Phoxinins, defined by the disconnection between temporal and preoperculomandibular sensory canals, is one of the eight clades in Leuciscinae. Consisting of Shiner, Chub, and Western clades (Fig.1), phoxinins include almost all North American minnows (excluding *Notemigonus crysoleucas* which belongs to the Eurasian leuciscins) and a few Eurasian genera (Cavender & Coburn 1992; Coburn & Cavender 1992).

The term "phoxinins" used in this publication has different content from that of "phoxinins" of Howes (1985). "Phoxinins" of Howes contains two genera, *Phoxinus* and *Couesius* (Howes 1985, 1991). When I refer to "phoxinins" of Howes, I use "phoxinins of Howes". The term "phoxinins" used herein refers to that of Cavender & Coburn (1992) and Coburn & Cavender (1992).

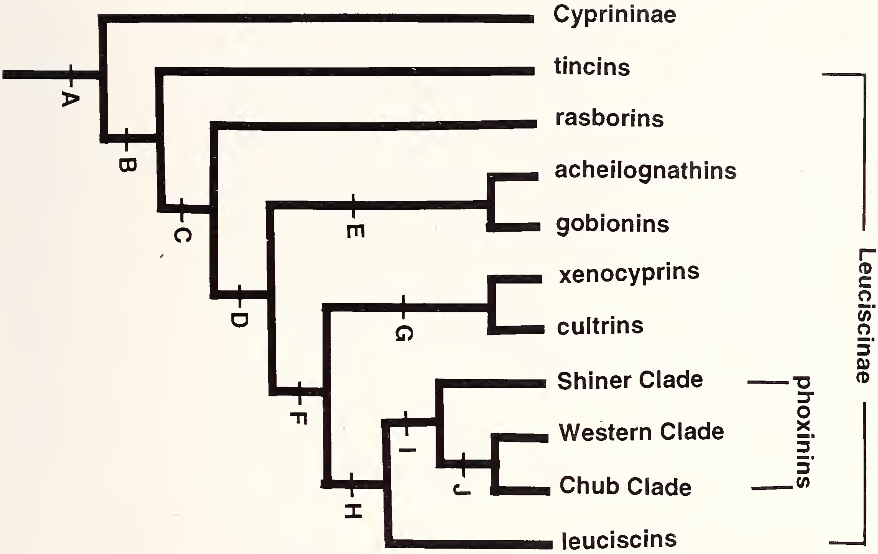

Fig.1: Phylogenetic hypothesis of Cyprinidae, showing the position of phoxinins. The synapomorphies supporting each nodes are as following. Node A: Absence of uncinate process on epibranchials I and II; subtemporal fossa deep and well-developed; interorbital septum formed by orbitosphenoid and a dorsal component of the parasphenoid. Node B: Rib head and parapophysis of fifth rib modified for greater mobility; origin of dorsal fin behind pelvic insertion; absence of anterior maxillary barbel and accompanying foramen in maxilla. Node C: Crest of neural complex (supraneural) divided dorsally (forked); anterior (free) supraneural in contact with neural complex; three unbranched dorsal fin rays. Node D: Scale without basal radii. Node E: Oval scales with modified circuli in posterior field and apical radii only. Node F: Pterotic elongated, its anterior end reaching in front of the anterior opening of the trigeminal-facial chamber. Node G: Anterior fork of the pelvic bone reduced; 48 diploid chromosomes with longest pair submetacentric. Node H: Supraorbital canal disconnected from the infraorbital canal; pharyngeal teeth in one or two rows. Node I: Phoxinin scale type; basal radii of scale absence; scale with numerous apical radii; infraorbital and preoperculomandibular canals not joined; opercular canal absent; preethmoid projecting anteroventrally when viewed anteriorly. Node J: Postorbital cranium elongated; anterior and posterior angles of pharyngeal arch rounded; rib of vertebra 4 with an anterior process (from Chen et al. 1984, Cavender & Coburn 1992, Coburn & Cavender 1992).

The Chub clade within the phoxinins (Fig.1) contains the Exoglossin clade, *Tribolodon*, and some other genera (Fig.2), including *Phoxinus*, defined as Hemitremian clade herein (see below for detail). The Exoglossin clade is well diagnosed by synapomorphies (Coburn & Cavender 1992) such as the shortened mandibular canal terminating posterior to the mental foramen. However, some problems are present in the relationships of other genera in the Chub clade [*Tribolodon* + Hemitremians] as discussed by Coburn & Cavender (1992). First, only two Eurasian genera of phoxinins (*Tribolodon* and *Rhynchocypris*) were studied, obviously, "the examination of additional Eurasian phoxinin genera is clearly required" (Coburn & Cavender 1992:329). Second, all the characters supporting the nodes below the Exoglossin clade in Coburn & Cavender (1992: Fig.13) are either re-

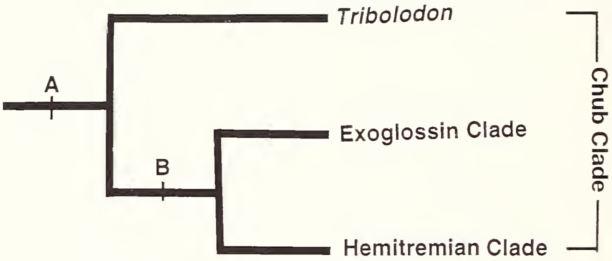

Fig.2: Phylogenetic hypothesis among the Chub Clade. The synapomorphies supporting the nodes are as following. Node A: Scale with apically directed lateral radii: distal lateral ethmoid hooked posteriorly; supraethmoid narrow: supraorbital small with irregular shape: neurocranium depressed with flattened parietal region and reduced orbitosphenoid septum: orbitosphenoid with extended parasphenoid contact. Node B: Postorbital cranium not elongated: weakly developed posttemporal fossa (from Coburn & Cavender 1992).

versed from other clades, reversed at the next few nodes, or vary intragenerically. Thus the phylogenetic relationships of these genera in the Chub clade (Chub clade excluding Exoglossin clade and *Tribolodon*) need to be further evaluated.

According to my results and those of Cavender & Coburn (1987), some North American and Eurasian minnow genera do form a monophyletic group, i.e., the Hemitremian clade, in the Chub clade of Coburn & Cavender (1992), as the sistergroup of the Exoglossin clade (Fig.2): whereas, the Hemitremian clade + Exoglossin clade (including *Platygobio, Hybognathus, Dionda, Campostoma, Macrhybopsis, Erimystax, Nocomis, Exoglossum, Phenacobius*) form the sistergroup of *Tribolodon* in the Chub clade (Fig.2).

The Hemitremian clade includes eight genera, i.e., *Phoxinus, Couesius, Semotilus, Hemitremia, Margariscus, Rhynchocypris, Eupallasella*, and *Lagowskiella*. All Hemitremians share one synapomorphy: the anterior placement of the anterior pterygiophores of the anal fin. In Hemitremians, the anterior few anal pterygiophores are placed forward to the first haemal spine, at least one anal pterygiophore is positioned anteriorly to the last rib (Fig.3B-C). Having studied all genera of exoglossins, other North America minnow genera, and some Eurasian minnow genera, I could not find this character from outside of the Hemitremian clade. Therefore, I interpret this character as an autapomorphy to support the monophyly of the clade. The anterior position of the anterior anal pterygiophores was first described and interpreted by Cavender & Coburn (1987) to support a monophyletic group including *Phoxinus, Margariscus, Semotilus, Hemitremia*, and *Couesius*. Later, Coburn & Cavender (1992) considered this character an evidence to support a monophyletic group including almost all the Chub clade (only *Tribolodon* excluded): and they interpreted the absence of this character in exoglossins as a reversal of the anterior placement of the anal pterygiophore(s).

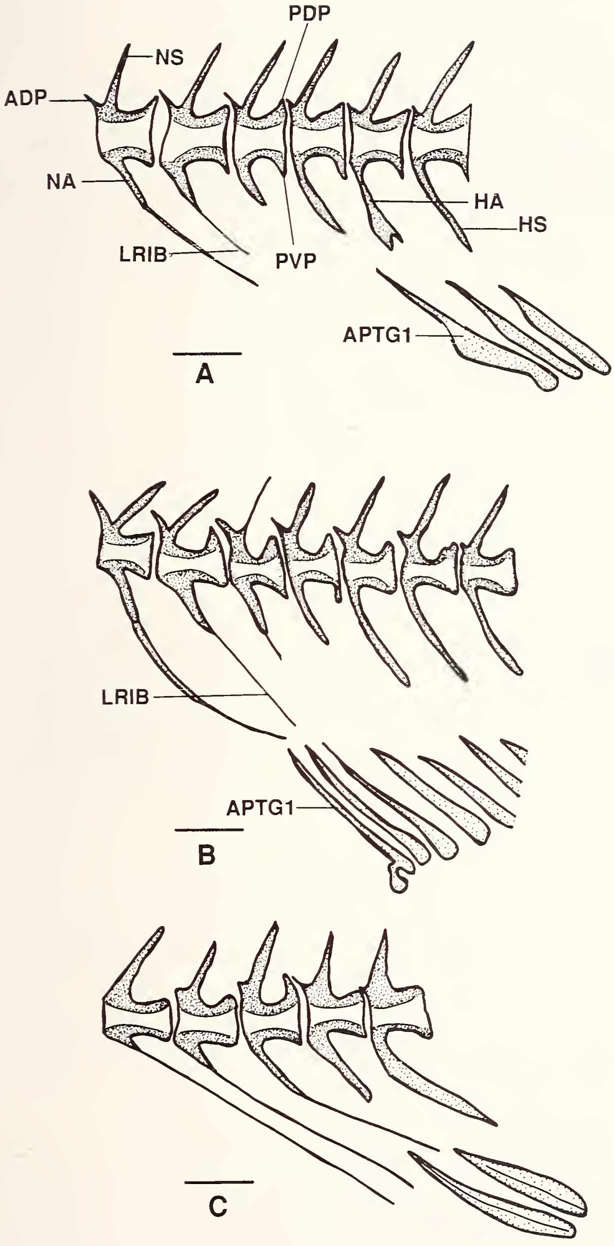

Fig.3: Anterior anal pterygiophores and associated vertebrae in hemitremians and in outgroup. A: *Nocomis platyrhynchus* (KU 18926, SL 46.5 mm); B: *Phoxinus phoxinus* (CNUC, uncat., 76 mm TL); C: *Hemitremia flammea* (KU 18931, 57.4 mm SL). Scale bars = 1 mm (for abbreviations see Appendix IV).

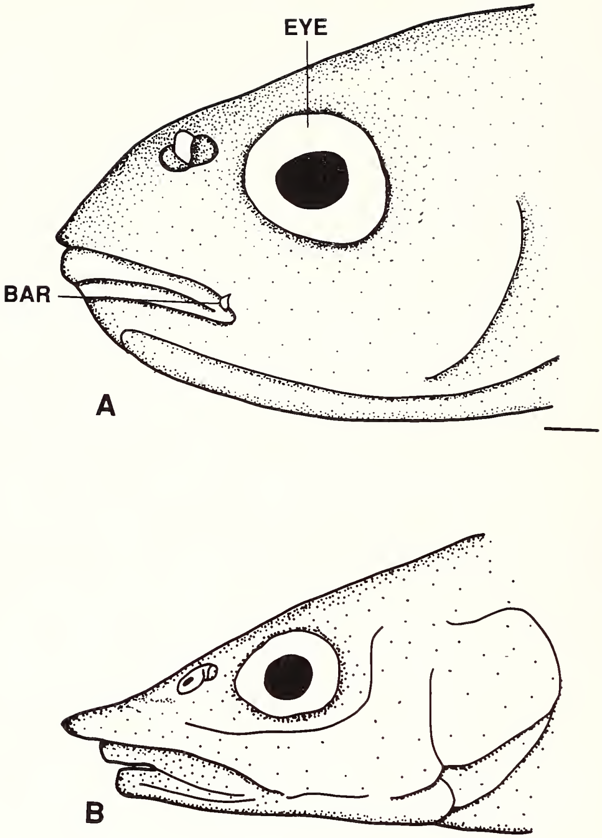

Fig.4: Profiles of lateral view of head of (A) *Couesius plumbeus* (KU 18965, 80.1 mm SL) and (B) *Rhynchocypris oxycephalus* (modified from Howes, 1985). Scale bar = 1 mm.

Analysis of transformation series in the Hemitremian clade

Based on the above discussion and Fig.2, the exoglossins are considered the first outgroup, and *Tribolodon* the second outgroup to polarize characters of the transformation series in the Hemitremian clade.

1. Fleshy rostral process (Fig.4A, B). The fleshy rostral process is an anterior flesh rostral extension. In the ingroups (except *Rhynchocypris*) and the outgroups, the rostral process

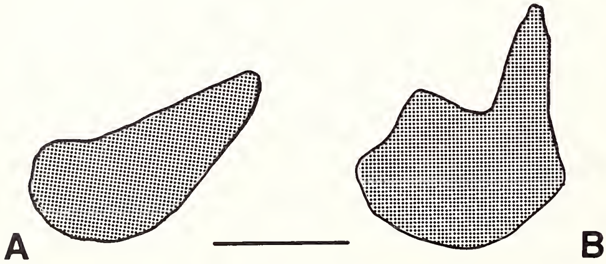

Fig.5: Anterior view of primary lamellae of (A) *Phoxinus oreas* (KU 3265, 56.7 mm SL) and (B) *Lagowskiella lagowskii* (NAIJ 14402, 95.8 mm SL). Scale bars = 1 mm.

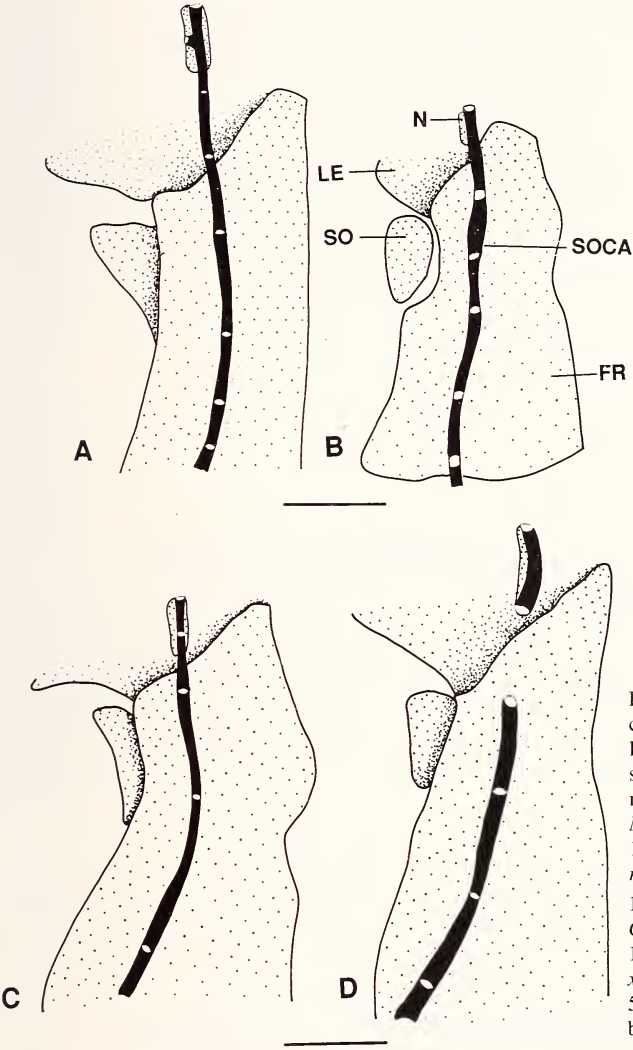

Fig.6: Part of the supraorbital canal (in black), and nasal, lateral ethmoid, frontal, and supraorbital bones in hemitremians and in the outgroup. A: *Nocomis platyrhynchus* (KU 18926, 46.5 mm SL); B: *Hemitremia flammea* (KU 18931, 57.4 mm SL); C: *Couesius plumbeus* (KU 18881, 65.0 mm SL); D: *Phoxinus erythrogaster* (KU 5773, 62.0 mm SL). Scale bars = 1 mm.

is very short (Fig.4A). In *Rhynchocypris*, the rostral process is long and well-developed (Fig.4B), especially in ripe females (Howes 1985). The process is also present in *Tribolodon hakonensis*, but the process in this species is less developed than that in *Rhynchocypris* (Cavender & Coburn 1992). The long fleshy rostral process was interpreted by Howes (1985) as an apomorphy for the genus *Rhynchocypris*. (This elongated rostral process is also present in *Rhinichthys*, Coburn 1994, pers. comm.). – **TS 1:** Fleshy rostral process very short [0], or long [1].

2. Posterior barbel (Fig.4A-B). The posterior barbel of *Couesius* is a papillate appendage derived from the upper rictal tissue which is not homologous with the barbels of other "barbeled cyprinids" (i.e., cyprinins) (Howes 1985). This posterior barbel is located at the corner of the mouth, and present in *Couesius* only (Fig.4A). – **TS 2:** A posterior barbel absent [0], or present [1].

3. Primary lamellae of the olfactory organ (Fig.5A-B). The primary lamellae of the olfactory organ are arranged at both sides (lateral and medial) of the axis in the olfactory

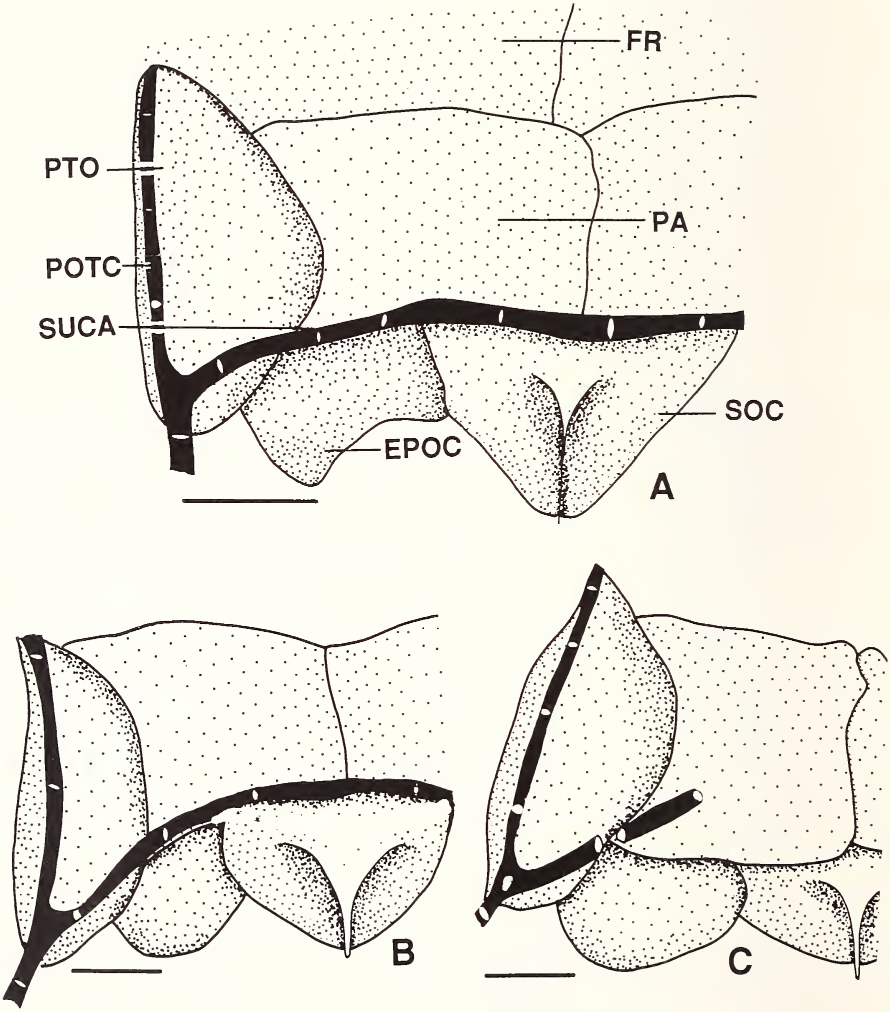

Fig.7: Supratemporal and otic canals (in black), frontal, pterotic, parietal, epioccipital, and supraoccipital bones in hemitremians and in the outgroup. A: *Nocomis platyrhynchus* (KU 18926, 46.5 mm SL); B: *Semotilus corporalis* (KU 18856, 58.0 mm SL); C: *Couesius plumbeus* (KU 18881, 56.6 mm SL). Scale bars = 1 mm.

organ. In *Rhynchocypris* and *Lagowskiella*, the dorsal margin of the primary lamellae bears a deep notch (Fig.5B); in the outgroups and other genera of the ingroups, the margin does not bear the deep notch (Fig.5A). – **TS 3:** A deep notch absent [0] or present [1] on the dorsal margin of the primary lamellae in the olfactory organ.

4. Supraorbital sensory canal (Fig.6A-D). The supraorbital sensory canal runs from the parietal posteriorly to the nasal bone anteriorly. It is interrupted into two portions, though the range of the gap might vary, between the anterior end of the frontal bone and the posterior end of the nasal bone in *Phoxinus* (Fig.6D). The canal is not interrupted at this region in other members of the ingroups and in the outgroups (Fig.6A-C). However, the interrupted canal is also found in *Cyprinus* and *Gila* of Cyprinidae (Cavender & Coburn 1992). – **TS 4:** Supraorbital sensory canal not interrupted [0], or interrupted [1] between the anterior end of the frontal bone and the posterior end of the nasal bone.

5. Supratemporal sensory canal (Fig.7A-C). In the outgroups, in *Rhynchocypris* and *Semotilus*, the left and right portions of the supratemporal sensory canal connect on the parietal (Fig.7A-B). Therefore, the supratemporal canal is continuous between the left and right portions of the canal. In other members of the ingroup, however, the canal is interrupted on the parietal. – **TS 5:** Left and right supratemporal sensory canals connect [0], or not connect [1] each other on the parietal.

6. Preopercular sensory canal (Fig.8 A-C). In the outgroups, in *Hemitremia, Rhynchocypris, Lagowskiella, Margariscus, Eupallasella*, and in *Semotilus*, the preopercular sensory canal extends upward and terminates at or near to the tip of the ascending arm of the preopercle bone (Fig.8A-B). In *Phoxinus* and *Couesius*, the preopercular canal terminates at about the middle of the ascending arm of the bone (Fig.8C).

Coburn & Cavender (1992) considered the "shortened preopercular canal" an evidence supporting the relationship of *Phoxinus* and other genera of the Chub clade. However, the

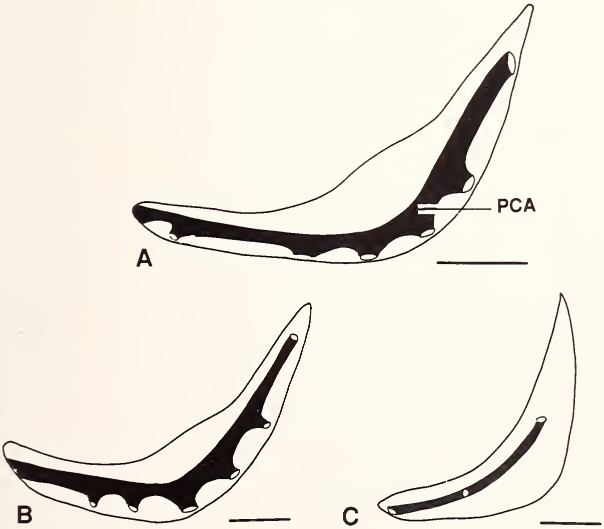

Fig.8: Preopercular canal (in black) and preopercle in hemitremians and in the outgroup. A: *Nocomis platyrhynchus* (KU 18926, 46.5 mm SL); B: *Semotilus corporalis* (KU 18856, 58.0 mm SL); C: *Phoxinus erythrogaster* (KU 5773, 62.0 mm SL). Scale bars = 1 mm.

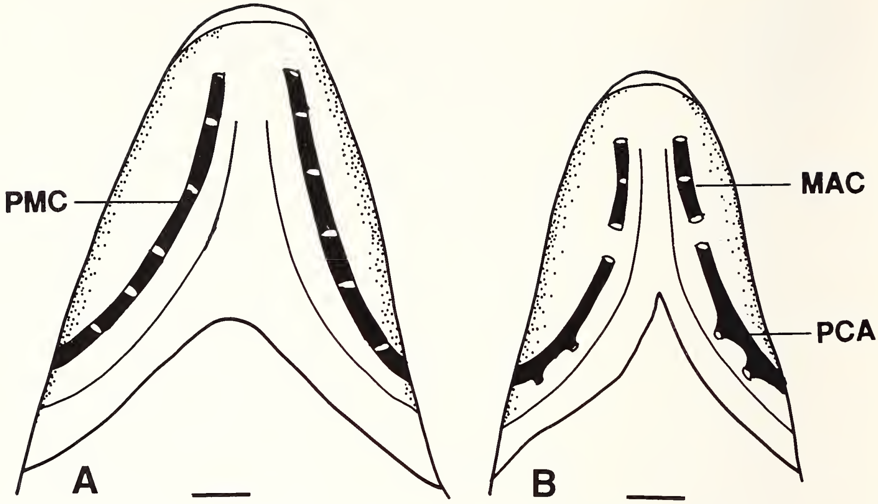

Fig.9: Ventral profile of heads of (A) *Couesius plumbeus* (KU 18965, 73.5 mm SL) and (B) *Phoxinus erythrogaster* (KU 10629, 62.5 mm SL), showing the preoperculomandibular canal (in black). Scale bars = 1 mm.

preopercular canal in *Phoxinus* is much shorter than that in other genera in the Chub clade. In other genera of the Chub clade (e.g., *Nocomis*), the canal ends near the tip of the ascending limb of the preopercle (Coburn & Cavender 1992). In *Phoxinus*, however, the canal terminates at the middle of the preopercle. – **TS 6:** Preopercular sensory canal terminates at or close to the tip [0], or at about the middle [1] of the ascending limb of the preopercle bone.

7. Preoperculomandibular canal (Fig.9A-B). In *Phoxinus*, the preoperculomandibular canal is interrupted between the posterior end of the mandibular portion and the anterior end of preopercular portion, thus the mandibular and the preopercular canals are formed (Fig.9B). This condition is not found in other genera of the ingroup or in the outgroups (Fig.9A). – **TS 7:** Preoperculomandibular canal continuous [0], or interrupted into two portions [1] between the mandibular and the preopercular bones.

8. Basal radii of scales (Fig.10A-C). Generally, scales of most cyprinids bear apical (posterior) radii only (Chu 1935) (Fig.10A). In the exoglossins of the Chub clade, no genus bears basal radii on the scales. Coburn & Cavender (1992) indicated that *Campostoma ornatum* bears basal (anterior) radii on the scale. However, no basal radii were found on the scales in the specimens of *C. ornatum* and *C. anomalum* I studied. In the Hemitremian clade, Coburn & Cavender (1992:352) mentioned the basal radii occurring within the Chub clade only in *Rhynchocypris* and *Phoxinus* of the taxa examined. However, my studies show that four genera in the Hemitremian clade, i.e., *Rhynchocypris, Lagowskiella, Eupallasella*, and *Phoxinus*, bear both basal and apical radii on their scales (Fig.10C). Basal radii are absent on the scales of *Semotilus, Couesius, Hemitremia*, and *Margariscus* of Hemitremians (Fig.10B). *Tribolodon* does not have basal radii (Chu 1935, Coburn & Cavander 1992).

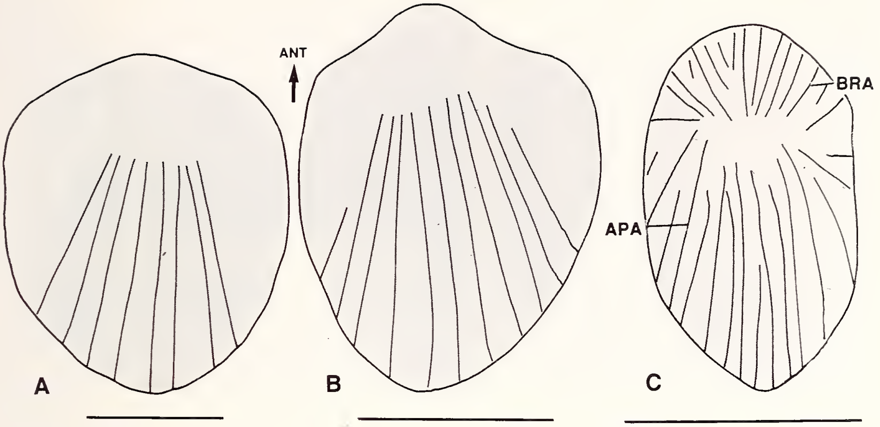

Fig.10: Scales on caudal peduncle in hemitremians and in the outgroup (only showing the general shape of the scale and the radii; circuli not presented). A: *Hybognathus placitus* (KU 2020, 61.6 mm SL); B: *Semotilus corporalis* (KU 16915, 55.4 mm SL); C: *Lagowskiella lagowskii* (MCZ 32370, 103.5 mm TL). Scale bars = 1 mm.

The presence of basal radii was first described by Cockerell & Callaway (1909) as one of the characters of *Phoxinus*. Chu (1935) considered the basal radii a useful character for the identification of some genera and species. In leuciscins [the sistergroup of phoxinins (Cavender & Coburn 1992)], *Rutilus* and *Leuciscus* have basal radii on scales (pers. observ.) that might be an evidence supporting the close relationship of these two genera among the leuciscines proposed by Chen (1987b). However, the arrangement of the radii of these two genera is different from that in the Hemitremian clade having basal and apical radii. In *Leuciscus* and *Rutilus*, the arrangements of both basal and apical radii are fan-shaped, and a large gap is present between the basal and apical radii. In the Hemitremians having basal radii, the radii are present on the entire scali and no gap is present between the apical and basal radii (Fig.10C). – **TS 8:** Scale bearing apical radii only [0], or bearing both apical and basal radii [1].

9. Shape of scales on the caudal peduncle (Fig.10A-C). In *Semotilus, Couesius, Margariscus, Hemitremia*, and in the outgroups, the scales on the caudal peduncle are relatively short, almost round (Fig.10A-B). In other members of the ingroup, the scales are elongated and rectangular-shaped (Fig.10C). – **TS 9:** Scales on caudal peduncle round [0], or elongated [1].

10. Breast scales of breeding male (Fig.11A-C). The term “breast scale” is defined according to Chen & Arratia (1996) as the scales at the region in front of the pectoral fin base, and posterior to the gill cleft. In most members of the ingroup and in the outgroups, the breast scales of breeding males are thin, relatively loose, and not deeply embedded (Fig.11A-B). In *Phoxinus*, however, the breast scales are much thicker and deeply embedded, and the apical (posterior) margins bear tubercles (Fig.11C).

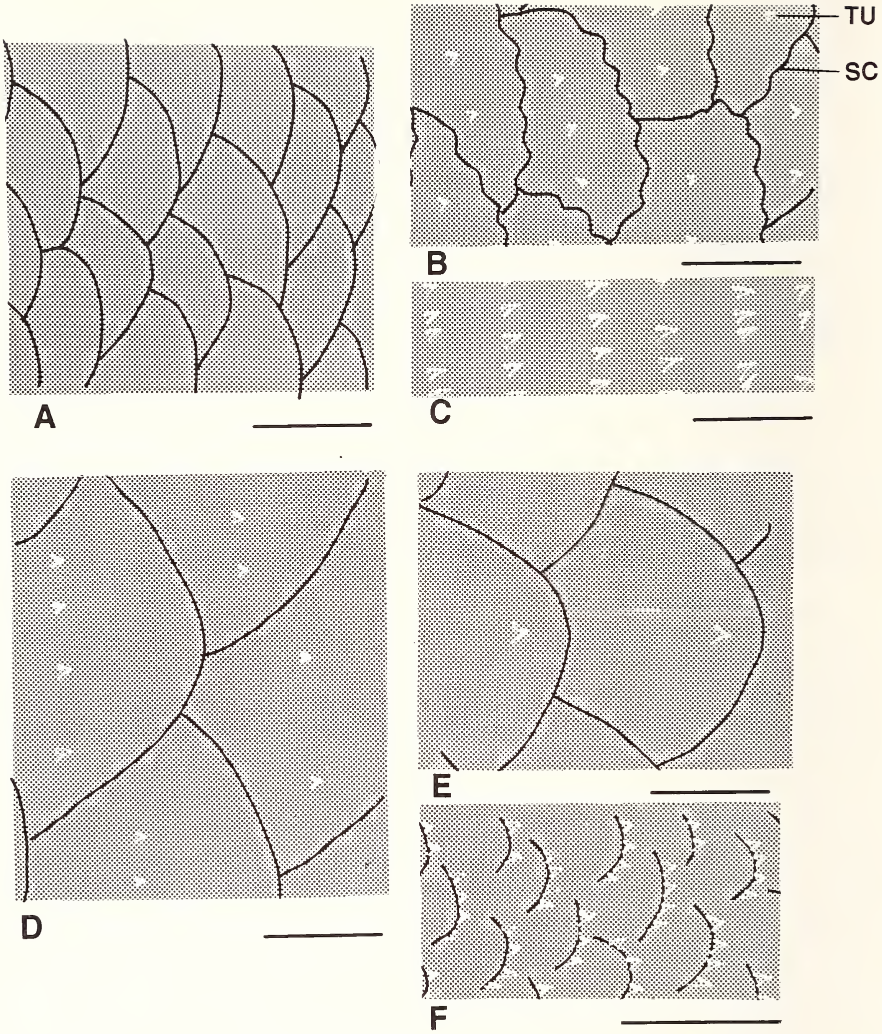

Fig.11: Breast scales and their tubercles (A-C, scale bars = 0.3 mm), and scales on caudal peduncle and their tubercles (D-F, scale bars = 1 mm) in breeding males in hemitremians. A: *Eupallasella percnurus* (MCZ 32369, 99.2 mm SL); B: *Margariscus margarita* (KU 8519, 102.5 mm SL); C: *Phoxinus oreas* (KU 3265, 43.5 mm SL); D: *Campostoma anomalum* (KU 20371, 121.5 mm SL); E: *Clinostomus funduloides* (KU 3262, 62.0 mm SL); F: *Phoxinus erythrogaster* (KU uncat., 47.0 mm SL).

In most members of the ingroup and in the outgroups, the breast scales have a smooth margin (Fig.11A). In *Couesius* and *Margariscus* of the ingroups, the apical (posterior) margin of the breast scales is serrated (Fig.11B). Having studied all genera of the outgroups, I did not find a similar condition on the breast scales in the outgroups. A serrated breast scale was illustrated in Howes (1985: Fig.2) for *Couesius*, but not discussed in his text. Our study also shows the serrated breast scales present in *Couesius* (Chen & Arratia 1996). – **TS 10:** Breast scales not deeply embedded [0], or deeply embedded [1] in breeding males. – **TS 11:** Apical margin of breast scales in breeding male smooth [0], or serrated [1].

11. Tuberculation on breast scales (Fig.11A-C). Based on our observation and published data, all cyprinids, except *Phoxinus*, lack tubercles on the apical margin of breast scales in breeding males (Chen & Arratia 1996). In *Phoxinus*, each breast scale bears a series of sharp tipped tubercles (generally two to six tubercles) on its apical margin (Fig.11C). Males of *Tribolodon hakonensis* also have a tuberculated margin in the breast scales, but the arrangement of the breast scales is different from that in *Phoxinus* (Cavender & Coburn 1992). I interpret the tuberculation in *Tribolodon* homoplastic with that of *Phoxinus* because of the different arrangement of breast scales of the two genera, and the lack of the anteriorly located anal pterygiophores in *Tribolodon* (Coburn & Cavender 1992).

In the outgroups, breeding males do not bear tubercles on the breast scales. In the ingroup, only three genera, *Margariscus, Semotilus*, and *Couesius*, bear one or two small tubercles at the middle of each scale, but no tubercles are present at the apical margin (Chen & Arratia 1996). The presence of centrally placed tubercles on the breast scales is interpreted as apomorphic, the absence of the tubercles on this area of scales as plesiomorphic.

Chen & Arratia (1996) summarize the history of the study on the tuberculation in *Phoxinus*. They compare the tuberculation on breast scales in *Phoxinus* and *Margariscus-Clinostomus-Couesius*-group of Hubbs & Brown (1929). According to Chen & Arratia (1996), two differences in breast tuberculation between *Phoxinus* and the *Margariscus-Clinostomus-Couesius*-group (defined as *Margariscus*-group hereafter) are present. (1) The breast scales are deeply embedded, and only the apical margin of the scale can be observed in *Phoxinus*; whereas the breast scales are loose, not deeply embedded, and most of a scale can be observed in the *Margariscus*-group. (2) In *Phoxinus*, tubercles are large, tall, sharp, and present at the apical margin of the breast scales, and each scale bears up to six tubercles (even more in some species of the genus); whereas in *Margariscus*-group, the tubercles are small, short, and centrally placed on the scale, and each scale bears only two to three tubercles.

TS 12: The breast scale in breeding males bearing no tubercles on the apical margin [0], or bearing a series of sharp-tipped tubercles at the apical margin [1]. – **TS 13:** Each breast scale of breeding males bearing no tubercle at its center [0], or centrally bearing one to three [1] small tubercles.

12. Tuberculation on scales on caudal peduncle (Fig.11D-F). In breeding males of most members in the ingroup and in the outgroups, each scale on the ventrolateral part of the caudal peduncle bears one or two tubercles on its middle portion, but no tubercles are present on its apical margin (Fig.11D-E). In *Phoxinus*, however, each scale in this region bears a few, up to 12, well-developed and sharp-tipped tubercles at its apical margin (Fig.11F). – **TS 14:** In breeding males, scales on the ventrolateral part of caudal peduncle bearing no tubercles on the apical margin [0]; or bearing two or more tubercles on the apical margin [1].

13. Frontal bone (Fig.6A-D). In *Hemitremia*, the anterolateral margin of the frontal bone bears a deep notch articulating with the supraorbital bone (Fig.6B): the lateral margin of the frontal does not bear the deep notch in other members of the ingroup and in the outgroups (Fig.6A, C, D). – **TS 15:** The anterolateral margin of the frontal articulating with supraorbital bone not forming a deep notch [0], or forming a deep notch [1].

14. Orbital septum (Fig.12A-E). The orbital septum is formed by fusion of the base of the left and right orbitosphenoids. An anterior process is present at the anterior margin of the orbital septum. The process is absent in outgroups and most members of the ingroups (Fig.12A, B, E); the process is present in *Semotilus*, *Hemitremia*, and *Eupallasella* (Fig.12C-D).

The orbital septum is high in most members of the ingroup and in the outgroups (Fig.12B-C), but lower in *Lagowskiella*, *Phoxinus*, and *Couesius* (Fig.12A, E).

In *Semotilus*, *Hemitremia*, *Phoxinus*, *Margariscus*, and in the outgroups, the orbital septum narrowly joins the dorsal side of the parasphenoid (Fig.12C, D-E); in other members of the ingroup, the septum broadly joins the parasphenoid (Fig.12A-B).

In most members of the ingroup and in the outgroups, no cartilage is present in front of the orbital septum in adult individuals (Fig.12A-B, D-E); in *Hemitremia* and *Eupallasella*, a short bar-shaped cartilage is present in front of the orbital septum (Fig.12C).

TS 16: An anterior process at the anterior margin of the orbital septum absent [0], or present [1]. – **TS 17:** Orbital septum high [0], or lower [1]. – **TS 18:** Orbital septum narrowly [0], or widely connecting with the dorsal side of the parasphenoid [1]. – **TS 19:** A cartilage absent [0], or present [1] in front of the orbital septum in adults.

15. Supraorbital bone. In *Hemitremia*, *Lagowskiella*, and in the outgroups, the supraorbital bone is large and well-developed; in other genera of the ingroup, the supraorbital bone is reduced to a narrow and short one.

Howes (1985) proposed presence of the small supraorbital bone as one of the synapomorphies of *Phoxinus*. My study shows that this character is widely distributed in several genera of Hemitremians. – **TS 20:** Supraorbital bone large [0], or small [1].

16. Basioccipital bone (Fig.13A-C). In *Phoxinus*, *Rhynchocypris*, *Campostoma*, *Dionda*, and *Hybognathus*, the pharyngeal pad of the basioccipital bone bears an anterior process (Fig.13C) (also see Mayden 1989, Schmidt 1989). In other members of the outgroups and ingroups, this process is absent (Fig.13B). However, in *P. neogaeus* and *P. brachyurus*, the process is absent as well. The absence of this anterior process in these two species is interpreted as a reversal of its presence, an apomorphy of these two species (see page 94 for the related discussion). – **TS 21:** The anterior process of the pharyngeal pad of the basioccipital bone absent [0], or present [1].

17. Parasphenoid bone (Fig.13D-E). The anterior part (in front of the ascending wing) of the parasphenoid in Hemitremians is dorsally bent. The angle α (Fig.13A) is herein defined as the angle between the horizontal line extending from the ventral side of the posterior part (posterior to the ascending wing) of the parasphenoid and the ventral side of the anterior part of the bone (anterior to the ascending wing). The larger this angle is, the greater the bent in the anterior part of the parasphenoid (Fig.13D). In *Hemitremia* and in

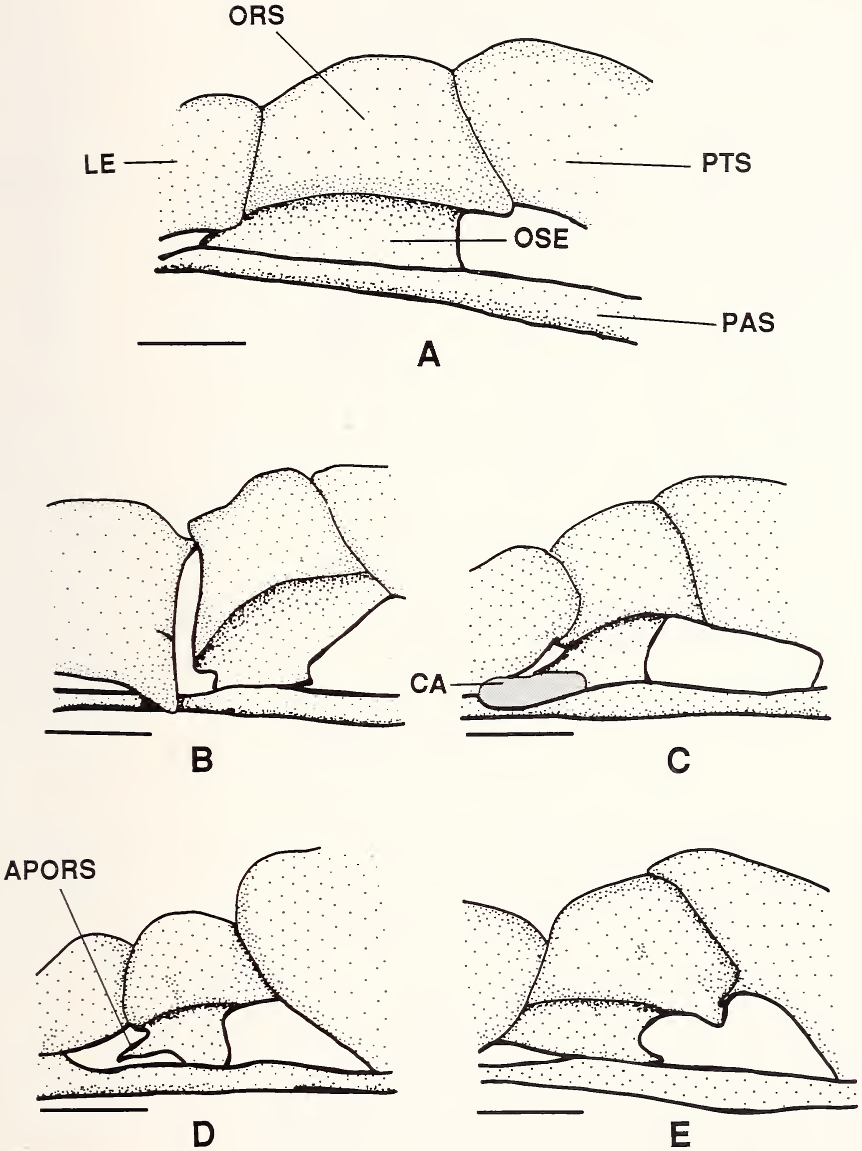

Fig.12: Diagrammatic lateral view of lateral ethmoid, orbitosphenoid, pterosphenoid, and parasphenoid in hemitremians and in the outgroup. A: *Lagowskiella lagowskii* (MCZ 32370, 103.5 mm TL): B: *Campostoma anomalum* (KU 3946, 61.0 mm TL); C: *Hemitremia flammea* (KU 18931, 55.9 mm TL); D: *Semotilus corporalis* (KU 18856, 58.0 mm TL); E: *Phoxinus neogaeus* (KU 8521, 53 mm TL). Scale bars = 1 mm.

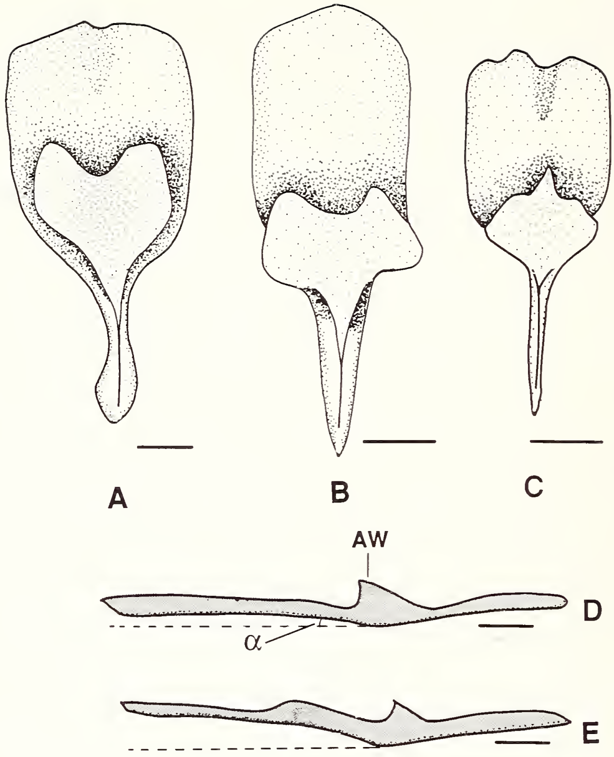

Fig.13: Basioccipital in ventral view (A-C), and parasphenoid in lateral view (D-E) in hemitremians and in the outgroup. A: *Platygobio gracilis* (KU 11950, 101.0 mm SL); B: *Couesius plumbeus* (KU 18881, 56.6 mm SL); C: *Phoxinus phoxinus* (CNUC uncat., 76.0 mm SL); D. *Hemitremia flammea* (KU 18931, 54.8 mm SL); E. *Phoxinus phoxinus* (CNUC uncat., 76.0 mm SL). Scale bars = 1 mm.

the outgroups, this angle is relatively smaller than that in other ingroups. – **TS 22:** Lateral view of the parasphenoid, angle α small [0], or large [1].

18. Quadrate bone (Fig.14A-C). Generally, in most ingroup and in the outgroups, the ventral margin of quadrate bears a very shallow concavity (Fig.14A, C). In *Margariscus*, the concavity is deep and narrow (Fig.14B). – **TS 23:** Ventral margin of the quadrate bearing a shallow and wide concavity [0], or a deep and narrow one [1].

19. Symplectic bone (Fig.14A-C). In most of the ingroup and in the outgroups, the dorsal margin of the symplectic bone bears a poorly developed process (or no process) articulating with the metapterygoid (Fig.14A, C). The process is better developed in *Margariscus* (Fig.14B) than that in other members of the ingroup and in the outgroups. – **TS 24:** Process at dorsal margin of the symplectic poorly [0], or well [1] developed.

20. Metapterygoid bone (Fig.14A-C). In *Couesius*, a deep notch is present at the posterior margin of the metapterygoid (Fig.14C). The notch is not present in other genera of the ingroup and outgroups (Fig.14A, B). – **TS 25:** A deep notch at the posterior margin of the metapterygoid absent [0], or present [1].

21. Opercle bone (Fig.15A-C). In most ingroup and outgroups, the anterodorsal process at the dorsal margin of the opercle is short and blunt (Fig.15A, B). In *Lagowskiella*, the

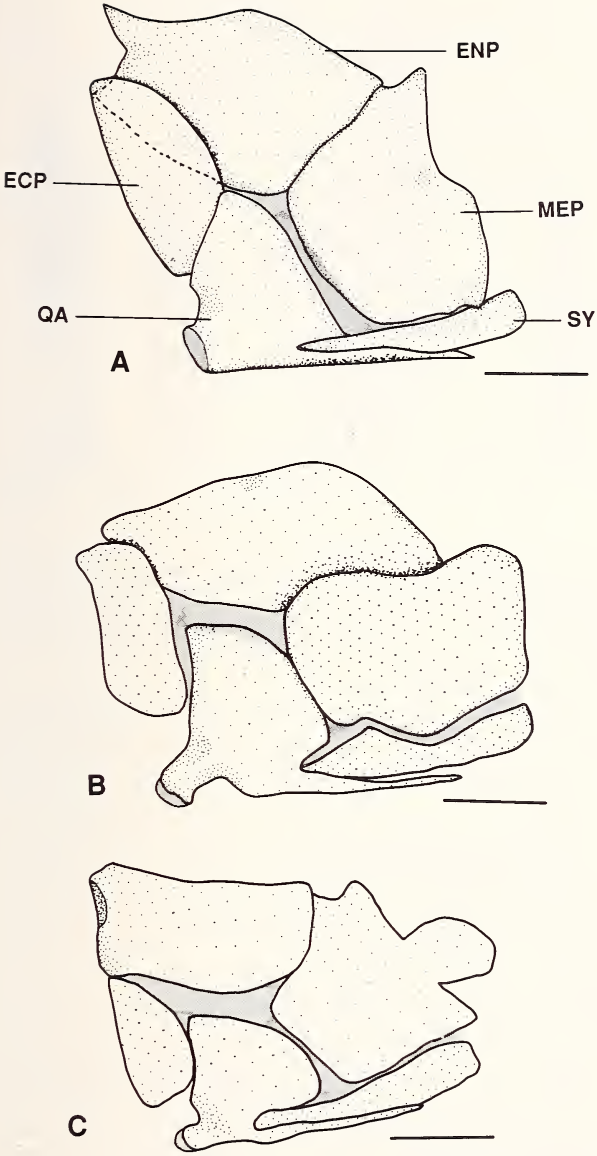

Fig.14: Lateral view of quadrate, symplectic, ectopterygoid, metapterygoid, and entopterygoid of hemitremians and outgroup. A: *Campostoma anomalum* (KU 3946, 61.0 mm SL); B: *Margariscus margarita* (KU 19000, 70.8 mm SL); C: *Couesius plumbeus* (KU 18881, 56.0 mm SL). Scale bars = 1 mm.

process is long and sharp (Fig.15C). – **TS 26:** Anterodorsal process of the opercle short and blunt [0], or long and sharp [1].

22. Supraneural bones (Fig.16A-C). In the ingroup and the outgroups, the supraneural bones are present in front of the dorsal fin origin. Supraneural bone 4 is the largest of all supraneurals. In *Semotilus, Lagowskiella*, and *Couesius* supraneural 4 is very large, and

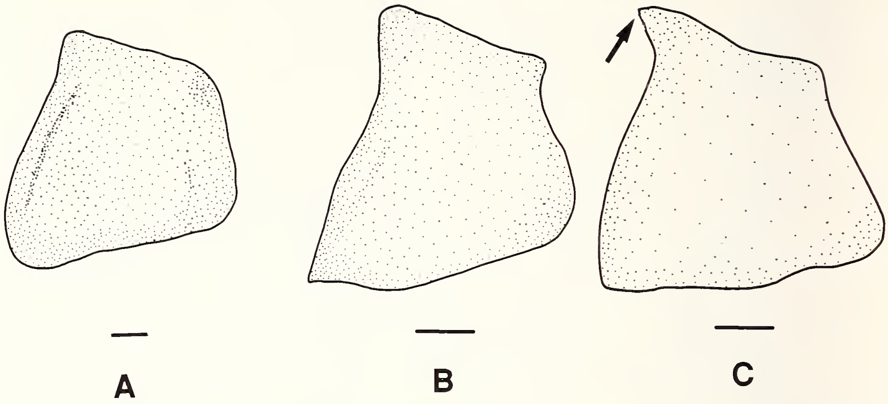

Fig.15: Opercle in lateral view in of hemitremians and in the outgroup. A: *Platygobio gracilis* (KU 11950, 101.0 mm SL); B: *Margariscus margarita* (KU 19000, 77.5 mm SL); C: *Lagowskiella lagowskii* (MCZ 32370, 103.5 mm SL). The arrow shows the anterodorsal process of the opercle. Scale bars = 1 mm.

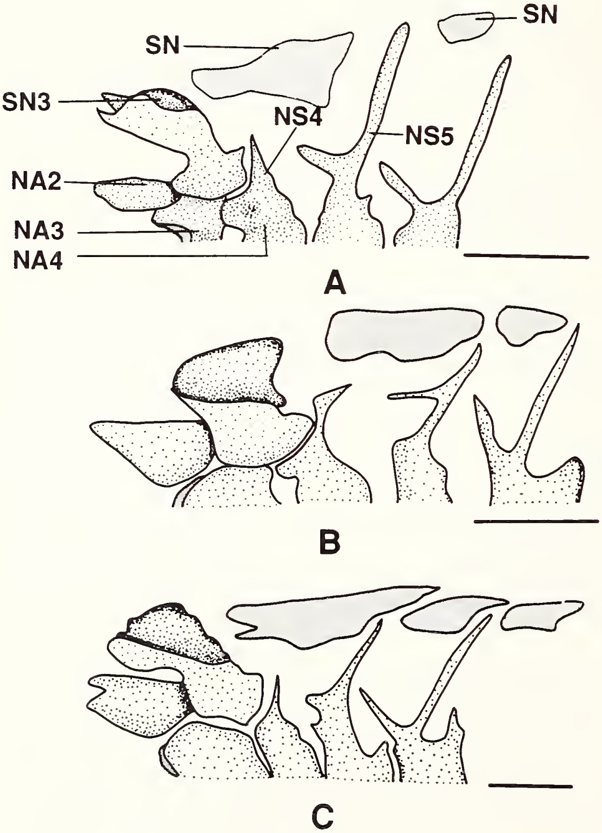

Fig.16: Lateral view of the neural arches and spines of the anterior vertebrae, the neural complex, and supraneural bones of some species of hemitremians and outgroup. A: *Dionda episcopa* (KU 7427, 38.0 mm SL); B: *Phoxinus issykkulensis* (P-10696, 42.4 mm SL); C: *Couesius plumbeus* (KU 18881, 56.6mm SL). Scale = 1 mm.

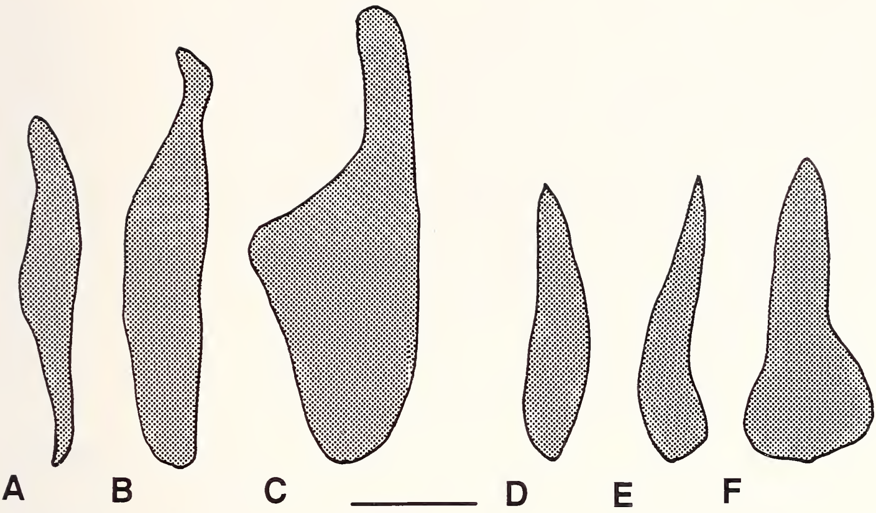

Fig.17: Lateral view of the posttemporal bone (A-C) and supracleithrum (D-F) of hemitremians and outgroup. A: *Campostoma anomalum* (KU 3946, 61.0 mm SL); B: *Couesius plumbeus* (KU 18881, 56.6 mm SL); C: *Hemitremia flammea* (KU 18931, 57.4 mm SL); D: *Dionda episcopa* (KU 16891, 54.1 mm SL); E: *Phoxinus cumberlandensis* (KU 18934, 52.0 mm SL); F: *Hemitremia flammea* (KU 18931, 57.4 mm SL). Scale bars = 1 mm.

extends from the dorsal margin of the neural complex to beyond the neural spine of the fifth vertebra (Fig.16C). In other genera of the ingroups and outgroups, the first supraneural bone is smaller (Fig.16A, B). – **TS 27:** Supraneural 4 small [0], or large [1].

23. Posttemporal bone (Fig.17A-C). Generally, the posttemporal bone is elongated and slender. In the outgroups and in most genera of the ingroup, the ventral portion of the posttemporal is slightly expanded (Fig.17A, B). In *Hemitremia*, however, the ventral portion of the bone is much larger than the dorsal portion of the bone (Fig.17C). – **TS 28:** Ventral portion of posttemporal bone slightly expanded [0], or broadly expanded [1].

24. Supracleithrum (Fig.17D-F). The supracleithrum is expanded at its middle portion. Therefore, the middle portion of the bone is slightly wider than its dorsal and ventral portions (Fig.17D-E). In *Hemitremia*, the supracleithrum is relatively short, the middle portion of the bone is extremely expanded, therefore, the middle portion is much wider than the ventral and dorsal portions of the bone (Fig.17F). – **TS 29:** Middle portion of the supracleithrum slightly expanded [0], or largely expanded [1].

Phylogenetic Relationships of the Hemitremian clade

Appendix I shows distribution of polarities of the 29 transformation series analyzed among the genera of the Hemitremian clade. Based on the matrix of Appendix I, PAUP (version 3.0) generated 135,135 trees with tree length from 43 steps to 57 steps. Two most parsimonious trees were generated with tree length = 43 steps, CI = 0.682 (CI excluding uninformative TS = 0.516), HI = 0.318 (HI excluding uninformative TS = 0.484), as shown

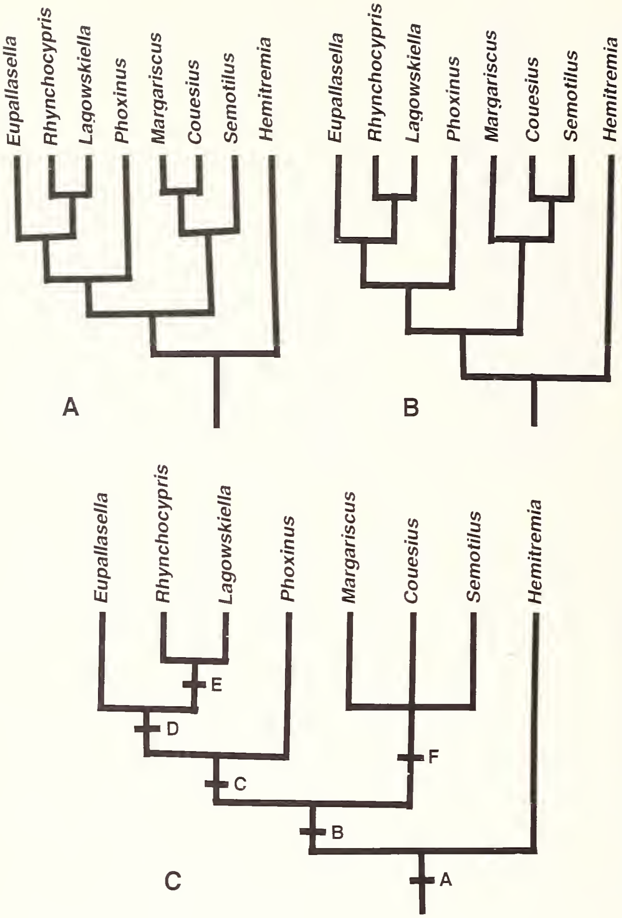

Fig.18: Phylogenetic hypotheses of relationships of the hemitremians. A. B: two equal most parsimonious trees: C: strict consensus tree of A and B. The synapomorphies supporting the nodes of tree C are as following. [The asterisk (*) at the right upper corner of the TS number marks the autapomorphy. The number following nodes A-F correspond to the transformation series (TS) number in page 26–39]: Node A: anterior placement of the anterior anal pterygiophores; Node B: 20. 22*; Node C: 8*. 9*; Node D: 18; Node E: 3; Node F: 13.

in A and B of Fig.18. A strict consensus tree was generated from these two trees (Fig.18C). The only difference between the two equal most parsimonious trees (Fig.18A, B) is the relationships among *Margariscus, Couesius*, and *Semotilus*. In tree A, *[Margariscus + Couesius]* is the sistergroup of *Semotilus*. In the tree B, *Margariscus* is the sistergroup of *[Couesius + Semotilus]*. The strict consensus tree (Fig.18C) shows an unresolved relationship of these three genera. The following discussion is based on the strict consensus tree (Fig.18C).

Two major clades are included in the Hemitremian clade: genus *Hemitremia*, and the *Phoxinus* clade including all the remaining genera of the Hemitremian clade.

The synapomorphies for each node of tree C (Fig.18:C) are given below in telegraphic form and include all changes on the node. The number of the transformation series is in parentheses followed by a brief description of the character. The asterisk (*) marks the autapomorphy. The apomorphies, the number of species, and the geographic distribution of each genus are briefly discussed under the related node.

Node A: This node unites all eight genera of the Hemitremian clade as a monophyletic group. All genera of the clade share the anteriorly positioned anterior anal pterygiophores.

Hemitremia Cope, 1870 is the sistergroup of the other seven genera of Hemitremians. Five apomorphies are present in the genus *Hemitremia*: (15*) anterolateral margin of frontal bearing a deep notch; (16) anterior margin of orbital septum forming an anteriorly directed sharp process; (19) a cartilage present infront of the orbital septum in adult; (28*) ventral portion of the posttemporal bone expanded; and (29*) middle portion of the supracleithrum expanded.

One species, *Hemitremia flammea* (Jordan & Gilbert), is in the genus which occurs in the tributaries of the middle Cumberland, upper Duke, and middle Tennessee River in Tennessee, Alabama, and Georgia (Boschung 1980).

Node B: This node unites the other seven genera of Hemitremians as a monophyletic group. Two synapomorphies are shared by these seven genera: (20) the supraorbital bone small (reversed in *Lagowskiella* and *Couesius*), and (22*) the parasphenoid relatively bent.

Node C: Four Eurasian genera, *Eupallasella, Rhynchocypris, Lagowskiella*, and *Phoxinus*, are united by node C. They share two synapomorphies: (8*) scale bearing both apical and basal radii; (9*) scale on caudal peduncle elongated.

These four genera were previously considered one genus, *Phoxinus* (e.g., Berg 1949). Howes (1985) separated *Rhynchocypris, Lagowskiella*, and *Eupallasella* from *Phoxinus*, and gave all of them generic status.

Eight synapomorphies are shared by the species of *Phoxinus*: (4*) supraorbital canal interrupted between nasal and frontal bones; (6) preopercular canal ending at middle of the ascending arm of the preopercle; (7*) preoperculomandibular canal interrupted into mandibular and preopercular canals; (10*) breast scales deeply embedded in breeding males; (12*) breast scales bearing a series of tubercles at its apical margin in breeding males; (14*) scales on caudal peduncle bearing three or more tubercles at the scale's apical margin in breeding males; (17) orbital septum lower; (21) pharyngeal pad of occipital bone bearing an anterior process.

Nine species are recognized in *Phoxinus* herein. Species of this genus occur in Eurasia and North America. See below for morphology, phylogenetic relationships, biogeography, and systematics of this genus.

Node D: This node unites three genera, *Eupallasella, Rhynchocypris*, and *Lagowskiella*, as a monophyletic group with one synapomorphy: (18) orbital septum widely connected to the dorsal aspect of the parasphenoid.

Eupallasella Dybowski, 1916 bears two synapomorphies: (16) anterior margin of orbital septum bearing an anterior process; (19) a cartilage present in front of the orbital septum in adult.

One species, *Eupallasella percnurus* (Pallas) is recognized by Howes (1985). This species occurs in northeast China (Yang & Huang 1964) and Korea (Berg 1949).

Node E: *Rhynchocypris* and *Lagowskiella* are united at this node by one synapomorphy: (3) dorsal margin of primary lamella of the olfactory organ bearing a deep notch.

Species of *Rhynchocypris* Günther, 1889 share the following three synapomorphies: (1*) long fleshy rostral process; (5) left and right supratemporal canal connecting on the parietal (reversal); (21) pharyngeal pad of basioccipital bearing an anterior process. According to Howes (1985), three species are included in the genus *Rhynchocypris*: *R. oxycephalus* Sauvage & Dabry, 1874, *R. steindachneri* Sauvage, 1883, and *R. costatus* (Fowler, 1899).

R. oxycephalus occurs in the tributaries of Chang Jiang River, northern China, western and Eastern Korea (Berg 1949, Huang & Yang 1964). *R. steindachneri* occurs in Japan and Korea (Jordan & Hubbs 1925). *R. costatus* occurs in Japan (Fowler 1899).

The following four synapomorphies are shared by *Lagowskiella* Dybowski, 1916: (17) orbital septum lower; (20) supraorbital bone large (reversal); (26*) anterodorsal process of the opercle long and sharp; (27) supraneural 4 large.

One species, *Lagowskiella lagowskii* (Dybowski, 1869), is recognized by Howes (1985). This species occurs in east Asia, such as Korea and northeast China (Berg 1949, Yang & Huang 1964).

Node F: This node corresponds to the trichotomy of *[Margariscus + Couesius + Semotilus]*. The three genera above this node share one synapomorphy: (13) one or two tubercles centrally present on each breast scale in breeding males.

Though the relationship of the three genera is unresolved in the strict consensus tree, the two equal most parsimonious trees (Fig.21A, B) resolve the relationship. The difference of relationships in Trees A and B (Fig.21A, B) is due to the different interpretation of two transformation series, TS 11 (shape of apical margin of breast scale) and TS 27 (size of the most anterior supraneural bone). In Tree A, TS 11[1] is considered a synapomorphy of *Couesius* and *Margariscus*, and TS 27[1] a homoplastic character in *Couesius* and *Semotilus*. In Tree B, TS 11[1] is interpreted a homoplastic character in *Margariscus* and *Couesius*, TS 27[1] a synapomorphy of *Couesius* and *Semotilus*.

Two apomorphies are found in the genus *Margariscus* Cockerell, 1909: (23*) presence of a deep notch at the ventral margin of the quadrate; (24*) the symplectic bearing a dorsal process.

A single species, *Margariscus margarita* Cope (in Günther 1868), belongs to *Margariscus* (Robins et al. 1991); it occurs in northern United States and Canada (Lee & Gilbert 1980). *M. margarita* used to be considered a species of *Semotilus* (e.g., Scott & Crossman 1973, Lee & Gilbert 1980). This species was recently separated from *Semotilus* (e.g., Johnston & Ramsey 1990, Coburn & Cavender 1992) because it is likely more closely related to *Couesius, Phoxinus*, or perhaps *Hemitremia* than to *Semotilus* (Robins et al. 1991). My study supports separation of the species from *Semotilus*, though the evidence does not support Robins et al. (1991). Neither of the two equal most parsimonious trees, nor the strict consensus tree show the sister group relationship of *Semotilus* and *Margariscus*.

Couesius Jordan, 1878 has seven apomorphies: (2*) presence of a posterior barbel; (6) preopercular canal ending at the middle of the ascending arm of the preopercle; (17) orbital septum lower; (18) orbital septum connecting broadly with the dorsal aspect of the parasphenoid; (20) supraorbital bone large (reversal); (25*) metapterygoid bearing a deep notch at its posterior margin; (27) the most anterior supraneural bone large. One species, *C. plumbeus* (Agassiz, 1850), is included in the genus (Robins et al. 1991), which mainly occurs in the western United States and Canada (Well 1980).

Semotilus Rafinesque, 1820a has three apomorphies: (5) the left and right portions of the supratemporal canal connected (reversal); (16) anterior margin of orbital septum forming an anterior process; (27) the most anterior supraneural bone large.

Four species, *Semotilus atromaculatus* (Mitchill, 1818), *S. corporalis* (Mitchill, 1817), *S. lumbee* Snelson & Suttkus, 1978, and *S. thoreauianus* Jordan, 1877 belong to *Semotilus*. The genus occurs mainly in eastern North America (Lee & Platania 1980, Gilbert 1980, Snelson 1980, Johnston & Ramsey 1990, Robins et al. 1991). A phylogenetic hypothesis of relationships among the four species of the genus was proposed by Johnston & Ramsey (1990).

Discussion

The relationships between *Phoxinus* and other minnow genera are an interesting and challenging problem that has attracted many ichthyologists' attention. At least four hypotheses have been proposed by previous authors through different approaches. My hypothesis on the phylogenetic relationships of *Phoxinus* with other genera (Fig.18C) differs from the previous ones. A brief discussion of the previous hypotheses is presented below.

Hypothesis 1: In a study of life history of *Clinostomus elongatus*, Koster (1939) noted that breeding males of *Clinostomus, Margariscus*, and *Couesius* had similar breast tuberculation. Koster (1939) therefore proposed a close relationship between *Phoxinus* and the group formed by *Margariscus, Clinostomus*, and *Couesius*. Koster (1939) correctly recognized the close relationships of *Margariscus* and *Couesius*. However, the breast tuberculation differs between *Phoxinus* and the group including *Margariscus* and *Couesius*, as discussed above. The breast tuberculation of *Clinostomus elongatus* is similar to that in *Margariscus* and *Couesius*, but this character might be homoplastic because *Margariscus* and *Couesius* are said to belong to the Chub clade, whereas *Clinostomus* belongs to the Shiner clade (Coburn & Cavender 1992).

Hypothesis 2: Like Koster (1939), Howes (1985, 1991) proposed a sistergroup relationship between *Phoxinus* and *Couesius* (forming the phoxinins of Howes) supported by the breast tuberculation. Two problems are present in this hypothesis. First, Howes did not recognize the observation that the breast tuberculation is also present in *Margariscus, Semotilus*, and *Clinostomus* (and he also seemed to be not aware of Koster's publication). Therefore, if the "breast tuberculation" of all genera bearing the tuberculation could be evaluated as homologous structures, more genera should be included in the phoxinins of Howes. Secondly, the breast tuberculation patterns of *Phoxinus* and *Couesius* are not similar one another (Chen & Arratia 1996). As discussed above, the breast tuberculation in the two genera should be evaluated as two transformation series. Therefore, the breast tuberculation does not support the sister group relationships of these two genera.

Hypothesis 3: Cavender & Coburn (1987) described the character of anteriorly positioned anal pterygiophores and proposed a monophyletic group including *Phoxinus, Semotilus, Couesius*, and *Hemitremia* based on this character. All these genera belong to the base of the Chub clade (Coburn & Cavender 1992). See "Monophyly of the Hemitremian clade and its position in the family Cyprinidae" for the discussion about this hypothesis.

Hypothesis 4: Instead of using breast tuberculation, Schmidt (1989) applied the anterior placement of the anterior anal pterygiophores discovered by Cavender & Coburn (1987) and proposed *Phoxinus* the sistergroup of *Semotilus*. However, this character is widely distributed among a few other genera, as discussed by Cavender & Coburn (1987), Coburn & Cavender (1992), and herein.

NON-OSTEOLOGICAL MORPHOLOGY

The morphological description and comparison among the species of *Phoxinus* are presented as two sections, the non-osteological and osteological morphology. In both sections, a brief review of the structure in cyprinids will be presented, followed by a detailed description of the structure in *Phoxinus* and the outgroup taxa (i.e., *Eupallasella, Rhynchocypris*, and *Lagowskiella*). Finally, a comparison among *Phoxinus* species and the outgroups, and a discussion on the polarity of the transformation series (TS) are presented. The number of transformation series in the Osteology is continuous with those in this section, and corresponds to the transformation series numbers in Appendices II and III.

Intraspecific variation will be discussed only in a few cases. Because of the ontogenetic variation of certain structures, the description and comparison among the species is based on similar-sized adult specimens. In a few cases young specimens are also used to obtain ontogenetic information.

External Morphology

Mouth (Fig.19A-C)

The mouth in cyprinids shows significant variation, such as mouth shape, width of the mouth opening (mouth gape), relative length of the upper and lower jaws, and morphology of the lower jaw. The mouth can be almost vertical (e.g., *Toxabramis houdemeri*), oblique (e.g., *Erythroculter dabryi*), or horizontal (e.g., *Xenocypris fangi*) (Wu 1964). The shape of the mouth can be partially demonstrated by degree of the mouth angle: the smaller the angle, the more horizontal the mouth; the larger the angle, the more oblique the mouth. The mouth gape can be large enough to reach below the middle of eye (e.g., *P. neogaeus*), or very small only approaching the anterior margin of the nasal opening (e.g., *Plagiognathops microlepis*) (Yang 1964).

In most cyprinids, the lower and upper jaws are almost equal in length (or the lower jaw is slightly shorter or longer than the upper one) (e.g., *Notropis* spp., *Xenocypris yunnanensis*); however, a much longer lower jaw (than the upper one) (e.g., *Luciobrama macrocephalus*), or a much longer upper jaw (e.g., *Varicorhinus tungting*) are also present in some species of the family. In most cyprinids, the structure of the mouth is relatively sim-

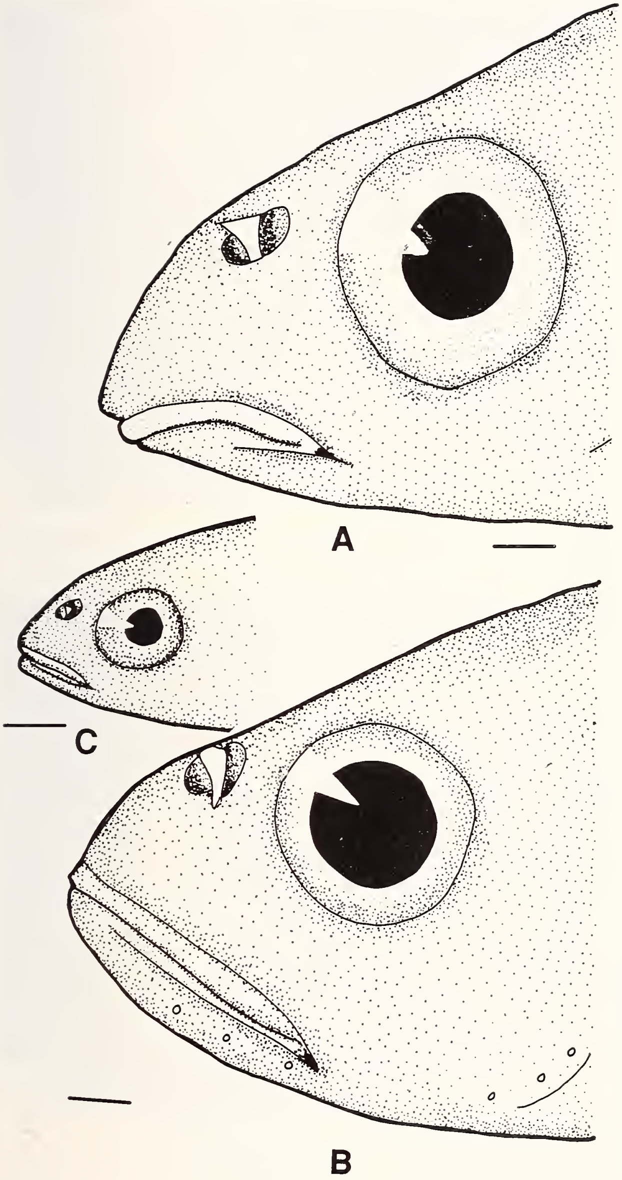

Fig.19: Diagrammatic lateral view of anterior portion of head of some species of *Phoxinus*. A: *P. oreas* (KU 3259, 61.6 mm SL); B: *P. neogaeus* (KU 14254, 55.4 mm SL); C: *P. neogaeus* (ANSP 5408, 20.0 mm SL). Scale bars = 1 mm.

ple (e.g., species of *Phoxinus*), however, in some species, the mouth, especially the lower jaw, presents a very complicated structure, such as a "sucking disk" (e.g., *Garra orientalis* – Nichols 1943).

Morphology of the mouth in *Phoxinus* is relatively simple. All *Phoxinus* species have a terminal or slightly subterminal mouth; the lower jaw is equal to, or slightly shorter than the upper one. No barbel is present (Fig.19 A-C). In *P. oreas* and *tennesseensis*, the mouth angle is small (≤55°) (TS 1[0]), so the mouth gape is horizontal. In other species, the mouth angle is large (≥60°) (TS 1[1]) (Fig.19B), and the gape is slightly oblique. In *P. neogaeus*, the mouth gape extends to below the middle of the eye's pupil (TS 2[1]); in other species of the genus, however, the gape never reaches the middle of the pupil (TS 2[0]). In the outgroups, the mouth angle is small (≤55°), and the mouth gape never extends to below the middle of the eye pupil.

The mouth angle and the gape length increase during growth in species of *Phoxinus*. For instance, in *P. neogaeus,* in a 20 mm standard length specimen, the mouth angle is small and the gape is short (almost reaching the anterior margin of eye); in a 55.4 mm standard length specimen, the angle is much larger and the mouth gape reaches middle of the pupil (Fig.19B, C). Phillips (1969a) showed the mouth of *P. erythrogaster* was less oblique than that of *P. eos*.

Olfactory organ (Figs. 20A-B, 21A-D)

Olfactory organ is a chemical receptor in fish, which can respond to chemical stimuli other than the qualities of sweet, bitter, salty and acid (Harder 1975). In all cyprinids, two nasal openings (anterior and posterior ones) are present on each side of the head. The anterior nasal opening is generally smaller than the posterior one. A nasal bridge is present between the anterior and posterior openings. In *Phoxinus*, the anterior opening is smaller and forms a short ellipse, and the posterior one is an elongated ellipse. No variation in shape of the nasal openings is observed in the genus *Phoxinus*.

A erect structure (nasal septum) is present from dorsal side of the bridge (Fig.20A, B). This nasal septum is an extension of the skin on the bridge. In *P. phoxinus, brachyurus*, and *neogaeus*, the dorsal side of the nasal septum is deeply concave (TS 3[1], Fig.20A); whereas, in *P. erythrogaster, cumberlandensis, tennesseensis, oreas, eos*, and *issykkulensis*, the nasal septum is not concave on its dorsal side (TS 3[0], Fig.20B) – a similar condition found in the outgroups.

The entire margin of the anterior nasal opening is erect (TS 4[0]) in most *Phoxinus* species and in the outgroups. In *P. erythrogaster*, the middle of the anterior margin is not erect (TS 4[1], Fig.20B).

Similar to the condition in most cyprinids, the olfactory organ in *Phoxinus* is composed of primary lamellae and axis (raphe). No secondary lamellae are present in *Phoxinus*. (In some cyprinids, e.g., *Parabramis pekinensis*, secondary lamellae are present on the primary ones – see Chen 1988b.) Numerous melanophores are present on both primary lamellae and axis.

Morphology of the axis and number of the primary lamellae vary ontogenetically. For instance, in *P. neogaeus*, the axis of the olfactory organ is very short and located at the anterior part of the organ, five primary lamellae are present in a 25 mm standard length individual (Fig.21D). In a 30 mm standard length individual, the axis is more elongated, almost reaching the middle of the organ, six primary lamellae are present. The axis is

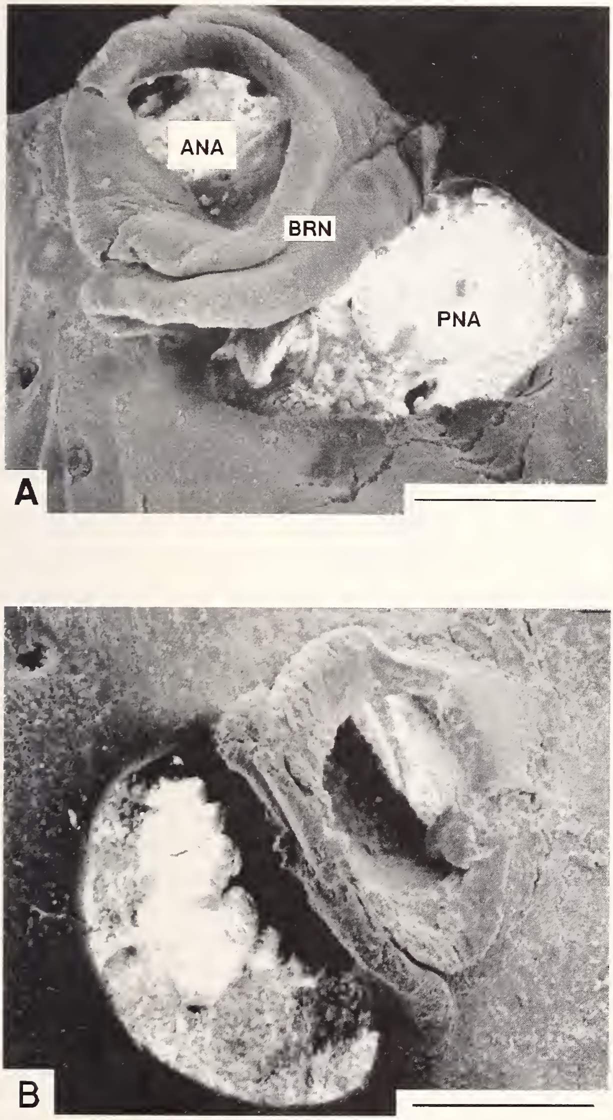

Fig.20: Nasal openings of (A) *Phoxinus phoxinus* (ZFMK, Series b, 80.5 mm SL), and (B) *P. erythrogaster* (KU 10629, 62.2 mm SL). Scale bars = 60 μm.

elongated, reaching middle of the organ, and the primary lamellae increase to eight by 51.8 mm standard length (Fig.21E). As a rule, the number of the primary lamellae increases ontogenetically until adult size is reached (Tab.1; Chen 1988b, Chen & Arratia 1994).

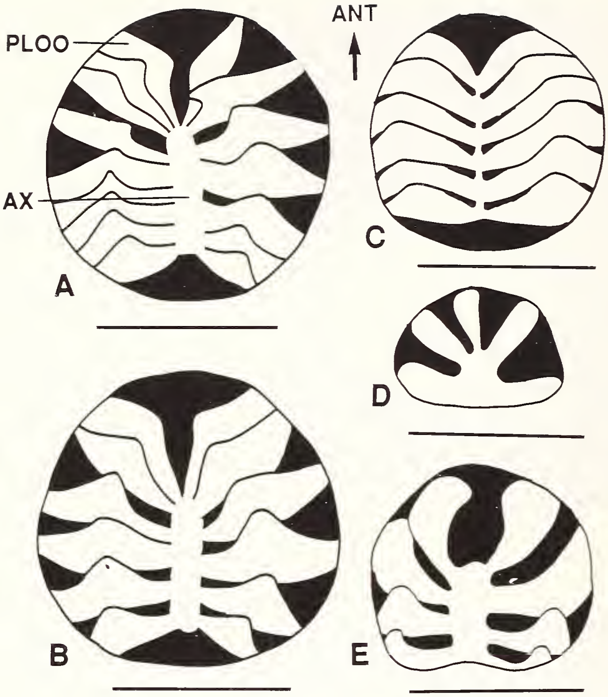

Fig.21: Diagrammatic dorsal view of the olfactory rosette of some species of *Phoxinus*. A: *P. phoxinus* (KU 22853, 56.4 mm SL); B: *P. erythrogaster* (KU 3895, 63.1 mm SL); C: *P. eos* (KU 4578, 41.8 mm SL); D: *P. neogaeus* (UT 44.2894, 25.0 mm SL); E: *P. neogaeus* (KU 14254, 51.8 mm SL). Scale bars = 1 mm.

Primary lamellae (Fig.21A-E): Chen (1988b) reported different shapes of primary lamellae in cyprinids, such as oar-shaped (e.g., *Saurogobio dabryi*), and hooked-shaped (e.g., *Diptychus pachycheilus*). Shape of the primary lamellae varies intra- and intergenerically in cyprinids (Chen 1988b). In adult specimens of *Phoxinus* species, the primary lamellae are oar-shaped and placed at the lateral and medial sides of the axis which is elongated and located at the median of the olfactory organ from the anterior margin to the middle of the organ. Variations of the primary lamellae are present in the shape of its dorsal margin and the number of the primary lamellae.

The dorsal margin of the primary lamellae is convex in the species of *Phoxinus*. Therefore the convex portion is higher than rest of the dorsal margin. In *P. phoxinus* and *erythrogaster*, the highest portion of the dorsal margin of primary lamellae is close to the axis (TS 5[1], Fig.21A-B). In all other species of *Phoxinus*, such as *P. brachyurus, neogaeus*, and in the outgroups, the highest portion is positioned off the axis (TS 5[0], Fig.21C).

Number of primary lamellae in adult individuals of the same species does not change significantly within species (Chen 1988b, Chen & Arratia 1994), though the number varies ontogenetically. In cyprinids the number of primary lamellae varies from 10 (e.g., *Phoxinus eos*) to 60 (e.g., *Mylopharyngodon piceus*) (Chen 1988b). In *Phoxinus*, the number of primary lamellae varies from 10 (*P. eos*) to 16 (*P. phoxinus*). In *P. phoxinus*, 16 primary lamellae are present (TS 6[1]); in all other *Phoxinus* species and in the outgroups, the number of the lamellae is 10-13 (TS 6[0]) (Tab.1).

Tab.1: Number (N) of primary lamellae of the olfactory organ in some species of *Phoxinus* with different standard length.

Species	SL(mm)	N	Species	SL(mm)	N
P. cumberlandensis	23.5	4	*P. neogaeus*	27.0	5
	42.0	10		34.5	8
	48.7	10		48.4	8
	50.9	9			
P. eos	26.4	7		52.0	11
	31.1	7			
	41.5	9	*P. oreas*	29.5	9
	41.8	9		33.5	9
	45.0	10		41.8	11
				43.1	10
P. erythrogaster	23.0	4		51.0	12
	26.0	6		53.4	13
	30.1	8			
	40.3	10	*P. phoxinus*	27.4	8
	46.5	12		46.8	10
	48.5	12		48.0	14
	50.2	12		60.1	16

Axis: Based on the shape of the axis, Chen (1988b) described six patterns of axes in cyprinids; i.e., Y, linear, elongated ellipsoidal, shorted ellipsoidal, bottle, and spindle patterns. Chen (1988b) proposed the elongated ellipsoidal pattern as plesiomorphic in cyprinids because this pattern is the condition present in most cyprinids, from which the shortened ellipsoidal, and linear patterns have derived independently.

Based on the number of primary lamellae and the shape of the axis, Yamamoto (1982) described eight types of olfactory organs in teleosts, lettered from A to H. Types F and G of the olfactory organ (Yomamoto 1982) are present in cyprinids. Chen & Arratia (1994) proposed 11 types (lettered from A to K) of olfactory organs in actinopterygians.

Extending from the anterior margin of the olfactory organ to the posterior portion of the organ, the axis is located at the middle portion of the olfactory organ in *Phoxinus*. Based on the criteria used by Chen (1988b), three morphological types of the axis can be described in *Phoxinus* as the following:

Elongated ellipsoidal type The axis is a narrow and elongated ellipse. This type is present in *Phoxinus phoxinus, oreas, erythrogaster, issykkulensis, tennesseensis,* and *brachyurus* (TS 7[0]; Fig.21A, B).

Linear type The axis is elongated, narrow and slender. This type is present in *Phoxinus eos* (TS 7[1]; Fig.21C).

Shorted ellipsoidal type The axis is wider, relatively short and elliptic in shape. This type is present in *P. cumberlandensis* and *neogaeus* (TS 7[2]; Fig.21E).

The elongated ellipsoidal type is present in the outgroups. According to the hypothesis on the relationships among different types of axes in cyprinids proposed by Chen (1988b)

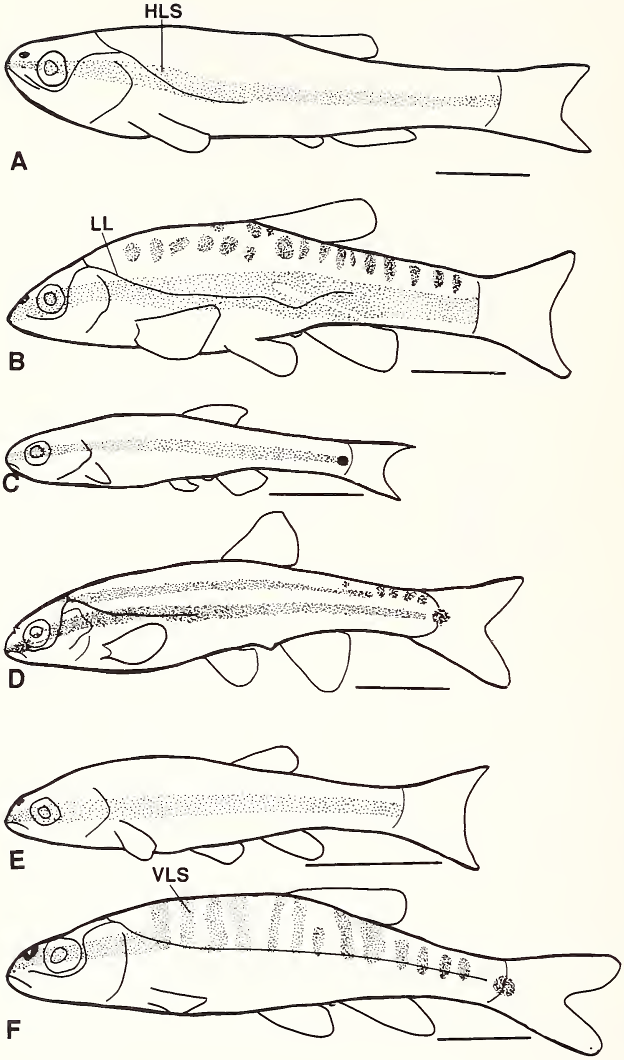

Fig.22: Lateral view of some species of *Phoxinus*, showing body lateral line and stripes. A: *P. neogaeus* (ANSP 48468, 51.0 mm SL); B: *P. oreas* (KU 3254, 47.6 mm SL); C: *P. erythrogaster* (KU uncat., 30.0 mm SL); D: *P. erythrogaster* (KU uncat., 46.0 mm SL); E: *P. phoxinus* (KU 22850, 27.4 mm SL); F: *P. phoxinus* (AMNH 71940, 52.1 mm SL). Scale bars = 1 mm.

and the outgroups comparison, I interpret the elongated ellipsoidal type the plesiomorphic condition, and the linear and the short ellipsoidal types of the axis independently derived from the plesiomorphic condition.

Lateral Line System (Fig.22A-F)

The lateral line system allows the fish to perceive a small pressure change in the surrounding water (Harder 1975). The lateral line system in cyprinids is composed of two sections, the cephalic and body lateral line. In cyprinids, the cephalic lateral line consists of infraorbital, supraorbital, otic, preoperculomandibular, and supratemporal canals (Reno 1969). The body lateral line can be incomplete (not extending to the base of the caudal fin, e.g., *Rhodeus sinensis*), or complete (terminated at the base of the caudal fin, e.g., *Rutilus rutilus*).

Cephalic lateral line. As discussed in previous section, three characteristics of the cephalic lateral line are present in *Phoxinus*.

1. The supraorbital canal is interrupted between the frontal and nasal bones (Fig.6D).
2. The preopercular canal extends up to the middle of the preopercular's ascending arm only (Fig.8C).
3. The preoperculomandibular canal is divided to the mandibular and the preopercular canals. These two portions do not connect with each other (Fig.9B).

Body lateral line (Fig.22A-F). All *Phoxinus* species bear the body lateral line which is continuous with the cephalic lateral line. The body lateral line in all species is interrupted in different regions and shows individual variations in the interruption.

Length of the body lateral line varies ontogenetically and phylogenetically. The body lateral line is shorter in young than in adults (Fig.22A-F). However, length of the body lateral line in adults has little variation in the same species. In *Phoxinus phoxinus, oreas, brachyurus, erythrogaster*, and in the outgroups, the body lateral line extends posteriorly to the caudal peduncle, even to the base of the caudal fin (TS 8[0]; Fig.22F); in other species of *Phoxinus*, the body lateral line reaches the middle flank between the origins of the pectoral and pelvic fins, or is even shorter (TS 8[1]; Fig.22A-B, D).

Genital Papilla (Fig.23A-D)

The genital papilla is present ventrally just anterior to the origin of the anal fin. Most *Phoxinus* species exhibit sexual dimorphism in the morphology of the genital papillae. Therefore, it is necessary to describe the papillae for the males and females separately.

Males (Fig.23B-C): The ventral surface of the genital papilla is smooth or bears a few skin pleats varying intraspecifically. In *Phoxinus tennesseensis* and *phoxinus*, the papilla bears a fleshy projection which extends beyond the anal orifice. In *P. tennesseensis*, the projection is short and blunt at its posterior end. In *P. phoxinus*, the projection is slender and longer. The projection is absent in other *Phoxinus* species. This projection is also present in *Rhynchocypris, Lagowskiella*, but absent in *Eupallasella* (Howes 1985). The projection is present in adult individuals only, not in young ones. Based on the ontogenetic data, I hypothesize presence of the elongated projection the apomorphic (TS 9[1]), and absence the plesiomorphic condition (TS 9[0]).

Females (Fig.23A, D): In all *Phoxinus* species, the ventral surface of the genital papilla bears skin pleats. The shape and number of the pleats vary individually. In *P. phoxinus*, a long and slender projection is present at the posterior end of the papilla (TS 10[1]). The projection is absent in the females of other *Phoxinus* species (TS10[0]). In some genera of the outgroups, e.g., *Rhynchocypris* and *Lagowskiella*, the papilla also bears a short projection, but in *Eupallasella* the projection is absent (Howes 1985). In *P. phoxinus*, the projection is absent in young specimens, and present in adult specimens. Based on the ontogenetic data, the presence of the long projection of the genital papilla in *P. phoxinus*

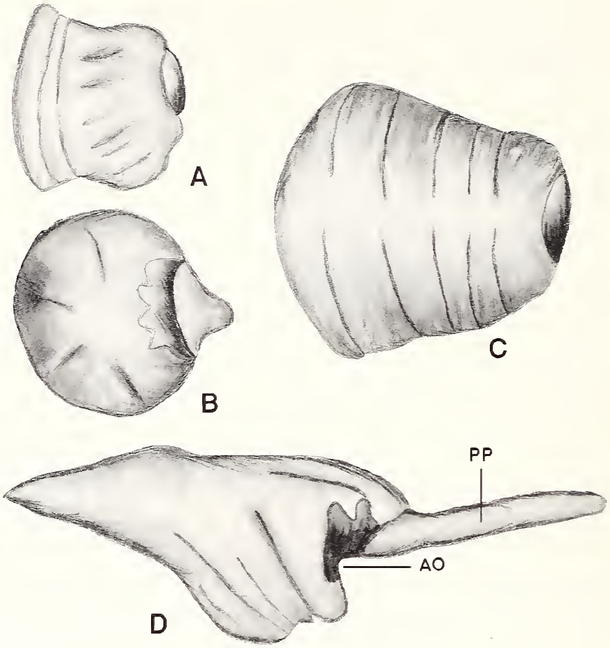

Fig.23: Ventral view of genital papillae of some species of *Phoxinus*. A: *P. cumberlandensis* (UT 44.1366, paratype, 56.8 mm SL, female); B: *P. oreas* (KU 3259, 55.9 mm SL, male); C: *P. tennesseensis* (UT 44.5274, 59.5 mm SL, male); D: *P. phoxinus* (ZFMK 585-586, 81.7 mm SL, female, lateral view). Scale bar = 1 mm.

is interpreted as apomorphic condition. Howes (1985) illustrated *P. phoxinus* as lacking the projection in both males and females. My observation differs from that of Howes (1985) in that a long projection is present in both genders of *P. phoxinus*.

Scales

In cyprinids, generally, scales cover the body, but the head is scaleless. All scales are cycloid and round to oval in shape. The margins of the scales are smooth, except for minor serrations in some species. The size of the scale varies from very large (e.g., *Cyprinus carpio*) to very small (e.g., *Phoxinus erythrogaster*). Similar to other cyprinids, the species of *Phoxinus* bear cycloid scales on the body, but no scale on the head. The scales in *Phoxinus* are very small and deeply embedded. They are more deeply embedded and smaller at the ventral aspect of the body than that at the body's lateral and dorsal sides.

The most distinguishing characteristics of scales in *Phoxinus* are the basal radii, and the elongate shape of the scales on the caudal peduncle. In *Phoxinus*, the radii are present almost evenly on the scale. The scale's focus is eccentric and close to the basal margin. No variation in radii, and shape of the scale is observed among *Phoxinus* species (Fig.10C).

Tuberculation

In cyprinids, breeding tubercles generally appear during the spawning season. Wiley & Collette (1970) studied fish breeding tubercles and listed at least 15 families belonging to four different orders that have breeding tubercles. Eight of the 15 families are in the order Cypriniformes. Using Scanning Electron Microscope (SEM), Roberts (1982) studied the unculi of ostariophysan fishes and showed the fine surface structure of some breeding tubercles in these fishes. Wiley & Collette (1970) proposed that the breeding tubercles have four primary functions: maintaining the body contact during spawning, defending the nest and/or territories, stimulating females in breeding or spawning periods, and recognizing a mate.

Similar to other cyprinids, both mature males and females of *Phoxinus* species bear breeding tubercles during breeding season. The breeding tubercles are much less developed in females than in males. SEM study demonstrated that the morphology of tubercles is highly diversified among the different regions of the same individual, and in the same region of different species (Chen & Arratia 1996). Based on the observations used SEM, they studied the distribution and fine surface morphology of the tubercles in *Phoxinus*, and recognized nine morphotypes, coded from A to I in *Phoxinus*. The following discussion is based mainly on Chen & Arratia (1996) and only for the transformation series analyzed herein. The readers are suggested to see this paper for details. Because no data on tuberculation are available in the outgroups, the exoglossin clade (Coburn & Cavender 1992) is used as the outgroups to determine the polarity of the transformation series.

Tubercles are present on the dorsal side of the head in all species of *Phoxinus*. *P. phoxinus* has type E tubercles which are large and few (TS 11[1]; Fig.24B). The dorsal side of head in *P. phoxinus* has four or five large tubercles surrounding the dorsal margin of the orbit, and two or three tubercles surrounding the nasal openings (TS 12[1]; Fig.24B). Tuberculation similar to that in *P. phoxinus* is also present in *Campostoma* but not in other minnows studied here. In all other *Phoxinus* species, tubercle type E is not found, but type A and B tubercles are present (TS 11[0]); the tubercles are small and numerous, and randomly present from the posterior margin of the occipital to the anterior end of the snout (Chen & Arratia 1996) (TS 12[0]; Fig.24A).

Type I is present on the pectoral fin in *Phoxinus erythrogaster* only (TS 13[1]), not found in other species (TS 13[0]). In *P. phoxinus*, the whole opercle bears a very high density of tubercles (TS 14[1]); whereas in other species of *Phoxinus* only part of the opercle

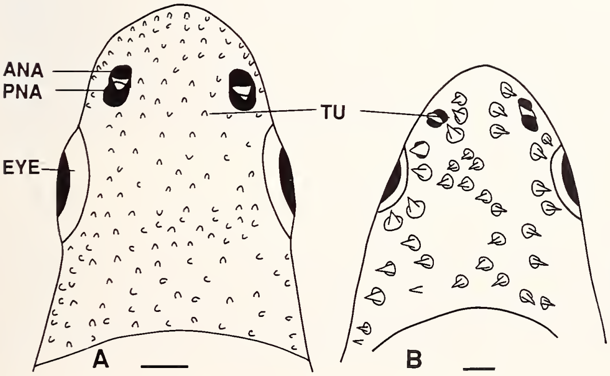

Fig.24: Dorsal view of heads of (A) *Phoxinus oreas* (KU 3259, SL 52.0 mm) and (B) *P. phoxinus* (ZFMK 657-659, 79.6 mm SL), showing distribution of tubercles on the dorsum of head. Scale bars = 1 mm.

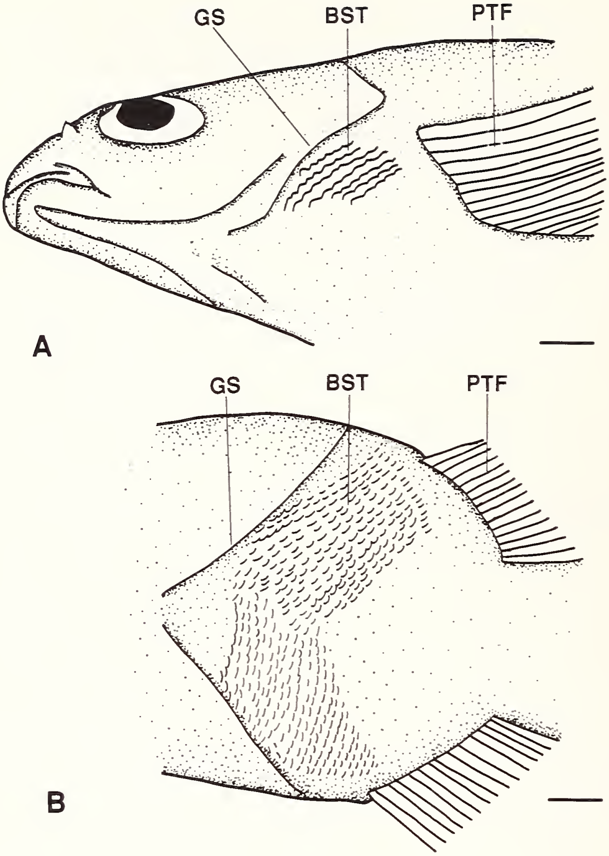

Fig.25: Profile of (A) lateral view of anterior body of *Phoxinus tennesseensis* (UT44.5274, 50.0 mm SL, male), and (B) ventral view of breast of *P. phoxinus* (KU 22859, 55.9 mm SL, female), showing the breast scales bearing tubercles. Scale bars = 1 mm.

bears tubercles at lower density (TS 14[0]) and some regions of the opercle have no tubercles (Chen & Arratia 1996).

On the ventral side of the body, tubercles are present only on the breast scales at the region anterior to the pectoral fin base and posteroventral to the gill cleft. The breast scales with tubercles are deeply embedded in *Phoxinus* species, as discussed previously. The tubercles are arranged as one row on the scale's apical margin. Except *P. cumberlandensis*, all other *Phoxinus* species bear less than 12 tubercles on the apical margin of each breast scale (TS 15[0]); whereas in *P. cumberlandensis*, each breast scale might have up to 16 tubercles (TS15[1]) (Chen & Arratia 1996).

In female *P. phoxinus*, the breast scales bear tubercles at their apical margin (Fig.25B). However, the tuberculation in the females is different with that in males (Fig.25A, B) (Chen & Arratia 1996). In female *P. phoxinus*, the breast scales are not deeply embedded, each scale bears about four small tubercles; in male *P. phoxinus* (and other species of *Phoxinus*), many more tubercles might be present on the apical margin of each breast scale. Tubercle type G is present in female *P. phoxinus* (TS 16[1]) which is not found in other species (males or females) (TS 16[0]) or male *P. phoxinus*. The breeding female *P. phoxinus* bears tubercles on the scales at the anterior portion (between the left and right breast scales) of the ventral part of the body (TS 17[1]) (Fig.25B). No tubercles are found in this area in other minnows (TS 17[0]) (Fig.25A) (Chen & Arratia 1996).

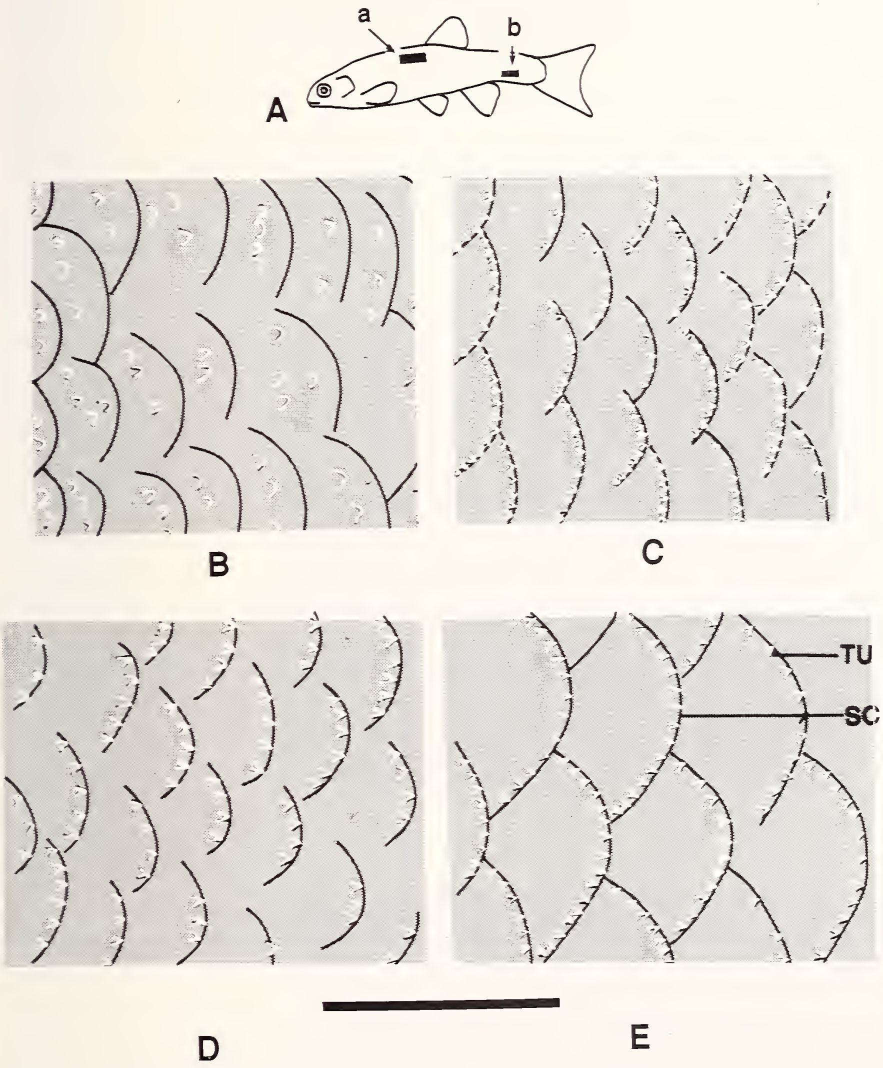

Fig.26: Scales of anterior lateral body (B-C), and of caudal peduncle (D-E) to show the distribution of tubercles on the scales of *Phoxinus*. A: A diagram showing the area presented in B-E (B-C: area a; D-E: area b); B: *P. cumberlandensis* (UT 44.4519, 50.0 mm SL); C: *P. phoxinus* (ZFMK 798, 65.5 mm SL); D: *P. erythrogaster* (KU 7300, 62.5 mm SL); E *P. phoxinus* (ZFMK 585-586, 81.7 mm SL). Scale bars = 1 mm.

In *P. phoxinus*, each scale on the anterior portion of the lateral body bears five to nine tubercles on the apical margin (TS18[1]) (Fig.26C). In other species, each scale bears one to four tubercles forward from the apical margin (TS18[0]) (Fig.26B).

In *P. phoxinus*, each scale on the lateral side of the caudal peduncle (especially at the ventrolateral portion of the caudal peduncle) bears up to 12 tubercles on the apical margin of the scale (TS 19[1]; Fig.26E). In other species of the genus, each scale on the caudal peduncle bears three to six tubercles on the apical margin (TS 19[0]; Fig.26D).

Tubercles on the dorsal side of the pectoral fin-rays are present in rows (Fig.27A, B). In *P. phoxinus*, tubercles are present from the second to sixth rays (total five rays) in three rows on each ray at the distal portion of the fin (TS 20[1]; Fig.27B). In other species, the tubercles are present from the second to fifth ray (total four rays), in two rows at the distal portion of the fin (TS 20[0]; Fig.27A) (Chen & Arratia 1996).

Few tubercles are present on the caudal fin rays in *P. phoxinus* (TS 21[1]), which are not found in other species of the genus (TS21[0]).

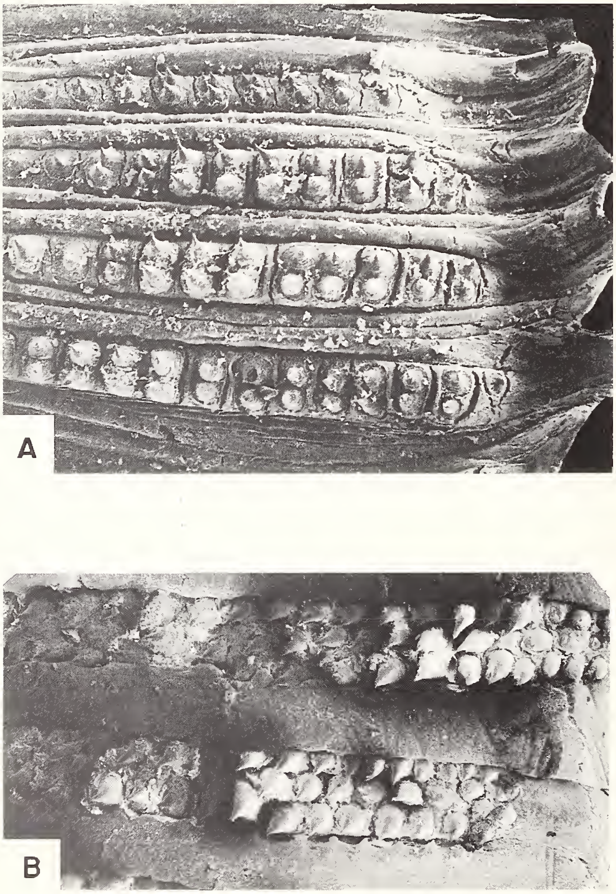

Fig.27: Tubercles on the dorsal side of the pectoral fin of (A) *Phoxinus oreas* (KU 3275,43.5 mm SL, scale bar = 1.0 mm), and (B) *P. phoxinus* (ZFMK 657-659, 79.6 mm SL, scale bar = 176 μm).

Coloration

Though coloration (or color pattern) of some cyprinids varies intraspecifically, the coloration of other cyprinids is useful for identification of the species (e.g., Yang & Huang 1964) and for phylogenetic analyses of some species or genera (e.g., Howes 1985). Color patterns for identification of the species include bands and stripes (number, shape, and location), speckles (size, shape, number and distribution), and the overall color of the body. However, as discussed by many authors (e.g., Heese 1981) and below, the color pattern might change ontogenetically and/or sexually in some species.

Generally, *Phoxinus* is a very colorful group of fishes. In fact, *P. erythrogaster* is considered by some authors to be the most beautiful North American freshwater fish (e.g., Forbes & Richardson 1920). All *Phoxinus* species bear either horizontal stripes or vertical bands (bars), or both.

The pigmentation described and compared below is based on alcoholic preserved adult specimens. The coloration of juveniles is mentioned in some cases for the ontogenetic change of the coloration in order to determine the polarity of the transformation series.

Numerous melanophores are irregularly present on the lateral body. In addition, all *Phoxinus* species bear vertical bands or horizontal dark stripes on the lateral body, and a dorsal dark stripe on the dorsum of the body extending from nape to in front of caudal fin. Based on the number, size, and shape of the stripes and bands on the lateral body, four types of the color patterns can be recognized on the lateral body in the *Phoxinus* species (Fig.22A-F).

1) *P. neogaeus*-type (Fig.22A): Only one uninterrupted horizontal stripe is present from the anterior end of the snout to the base of the caudal fin along the middle of the lateral body. The stripe is almost equal in width along its length. This type is present in *P. neogaeus, cumberlandensis, issykkulensis*, and *brachyurus*. In young individuals of *P. cumberlandensis*, the stripe is narrow and almost equal in width along its length (similar to other species in this type), but it is much broader in adults of the species.

2) *P. oreas*-type (Fig.22B): Lateral body bears one horizontal stripe and a few vertical bands. This type is observed in *P. oreas* only. The vertical bands are dorsal to the horizontal stripe which is interrupted into two sections (anterior and posterior section) at about the position of the anal fin. The anterior section of the horizontal stripe gradually curves down to base of the anal fin.

3) *P. erythrogaster*-type (Fig.22D): Lateral body bears two horizontal stripes without vertical bands. This type is present in *P. erythrogaster, eos*, and *tennesseensis*. In these species the lower horizontal stripe is broader and longer than the upper one. The lower one extends from the anterior end of the snout to the base of the caudal fin. In *P. erythrogaster* and *eos*, the upper strip is broken into blotches along the caudal peduncle.

4) *P. phoxinus*-type (Fig.22F): Lateral body has about 10 to 15 vertical bands without horizontal stripes. All vertical bands are almost equal in width, as well as the spaces between two bands. This type is present in *P. phoxinus* only.

The dorsal portion of the lateral body (dorsal to the lateral stripe) bears a few big speckles in *P. brachyurus* and *P. oreas*.

One horizontal stripe is present on lateral body in the outgroups. In all members of the ingroup, no matter what pigmentation pattern a species might bear in adults, young specimens (or larvae) always bear one horizontal stripe of equal width along the length of the lateral body (Fig.22C, E). The dorsal horizontal stripe (if any) appears later onto-

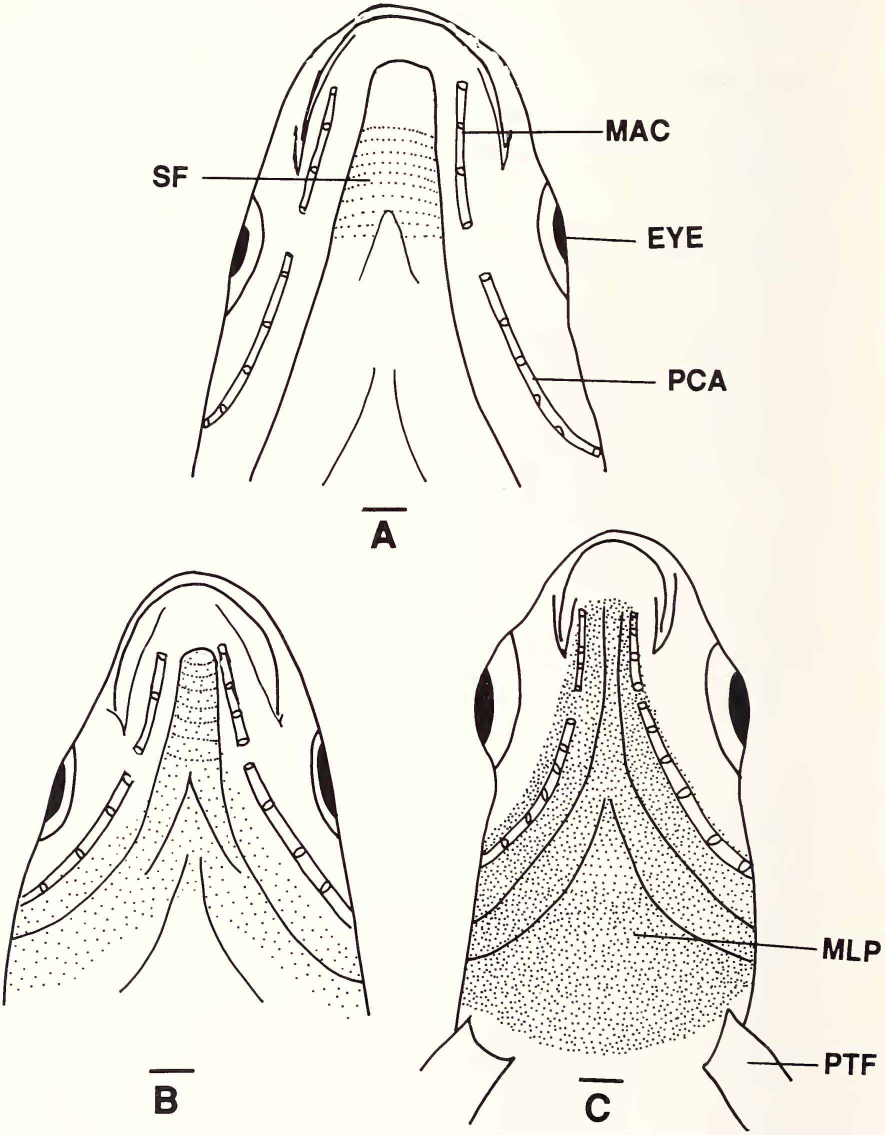

Fig.28: Profiles of ventral view of head, showing the distribution of melanophores. A: *Phoxinus neogaeus* [CA (SU) 09835, 59.5 mm SL]; B: *P. phoxinus* (KU 22860, 57.2 mm SL); C: *P. oreas* (KU 22257, 42.5 mm SL). Scale bars = 1 mm.

genetically. According to Tack (1940a), the vertical bands in *P. phoxinus* are resulted from the interruptions of the horizontal stripe. Therefore, based on the ontogenetic evidence and outgroup comparison, the *P. neogaeus*-type is hypothesized to be plesiomorphic (TS 22[0]), and other types to be apomorphic condition. Because no evidence is found to demonstrate how the apomorphic types are derived, I interpret the apomorphic conditions as independently derived from the *P. neogaeus*-type (*P. erythrogaster*-type: TS 22[1]; *P. phoxinus*-type: TS 22[2]; *P. oreas*-type: TS22 [3]).

The outgroups and most of the ingroup do not bear large speckles at the dorsal region of the lateral body (TS 23[0]). Therefore, the presence of the large speckles in *P. oreas* and *brachyurus* is proposed to be apomorphic (TS 23[1]).

In *P. brachyurus, neogaeus, issykkulensis, eos*, and *erythrogaster*, no (or very few) melanophores are present at the isthmus or the anterior portion of the breast (TS 24[0]; Fig.28A). In *P. phoxinus*, melanophores are present at the isthmus only (TS 24[1])

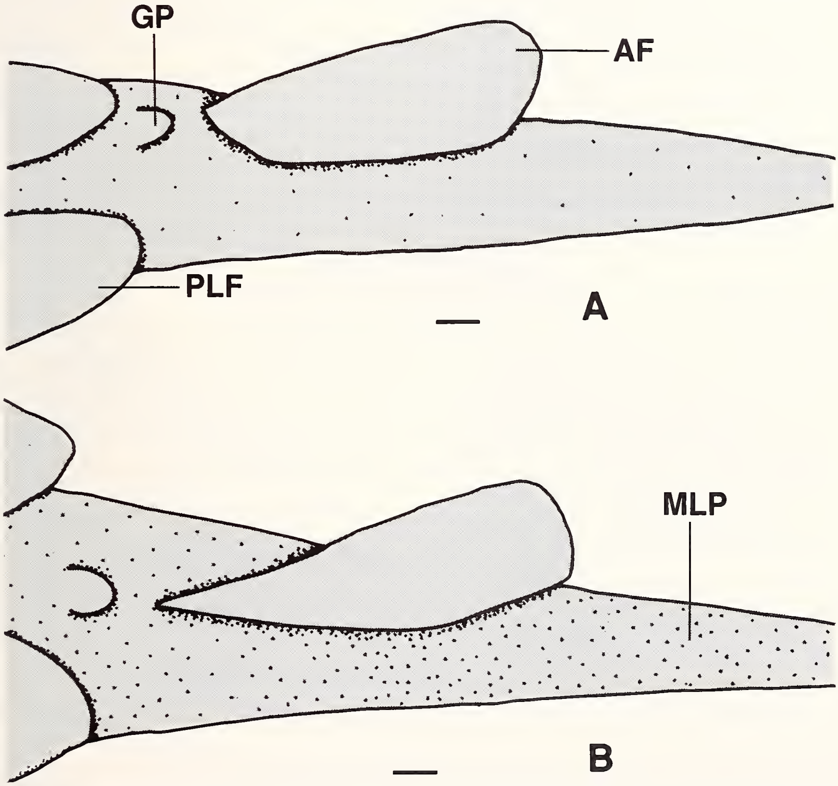

Fig.29: Diagrammatic profiles of ventral view of caudal peduncle of (A) *Phoxinus phoxinus* (KU 22860, 60.0 mm SL), and (B) *P. tennesseensis* (UT 44.5274, 58.5 mm SL), showing the distribution of the melanophores. Scale bars = 1 mm.

(Fig.28B). In *P. oreas, tennesseensis*, and *cumberlandensis* melanophores are present on both isthmus and breast (TS 24[2]; Fig.28C).

No melanophore is present on the isthmus and breast in the outgroups. In some young *P. oreas*, melanophores do not extend as far posteriorly as in adults. Thus the absence of melanophores (at both isthmus and breast) is hypothesized to be the plesiomorphic condition, the presence of melanophores at the isthmus, and the presence of melanophores on both isthmus and breast to be the apomorphic conditions.

No (or very few) melanophores are present on the belly in *Phoxinus* species. However, numerous melanophores are present on the ventral surface of the caudal peduncle in *P. brachyurus, neogaeus, issykkulensis*, and *tennesseensis* (Fig.29B). The presence of these melanophores is apomorphic (TS 25[1]) in comparison with the outgroups which do not bear melanophores in this region (TS 25[0]).

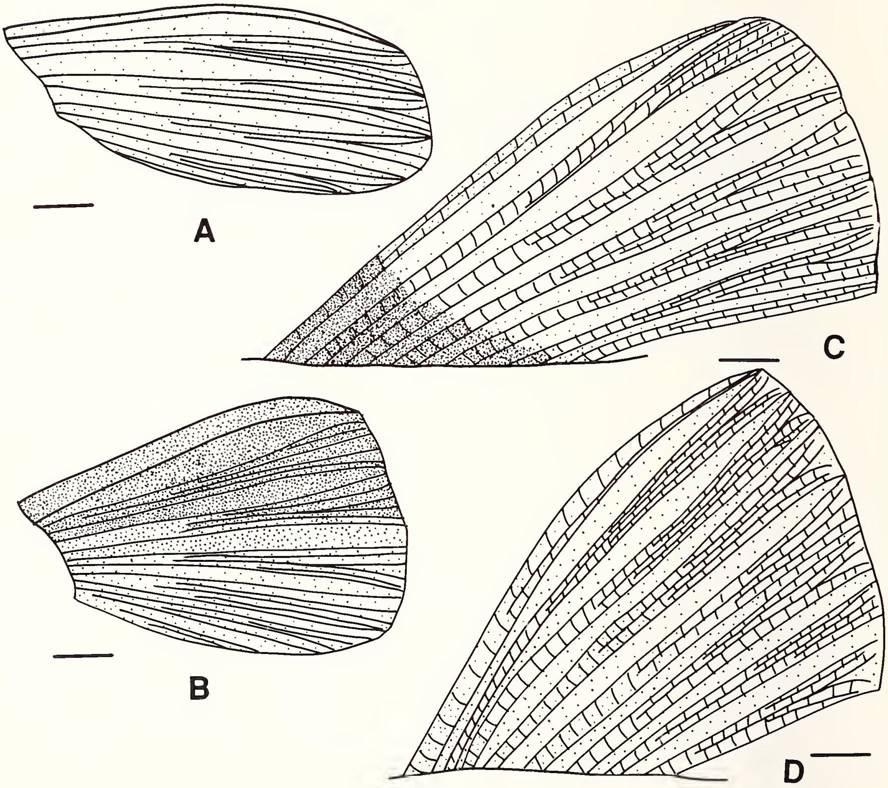

Fig.30: Profiles of dorsal view of pectoral fin (A-B), and lateral view of dorsal fin (C-D) of species of *Phoxinus* showing the distribution of the melanophores on the fins. A: *P. neogaeus*, unbreeding male (ANSP 48468, 59.7 mm SL); B: *P. neogaeus*, breeding male (UT 44.2870, 49.0 mm SL); C: *P. erythrogaster* (KU 7300, 59.5 mm SL); D: *P. tennesseensis* (UT 44.5274, 58.8 mm SL). Scale = 1 mm.

Similar to the outgroups, all *Phoxinus* species have a dark dorsal stripe at the dorsum of the body from the nape to in front of the caudal fin. No significant variation of the stripe is present in *Phoxinus*.

The first to sixth pectoral fin-rays and the interradial membrane between the rays bear melanophores. The first ray has more melanophores than the remaining (Fig.30A, B). Rays and membrane behind the sixth ray bear few melanophores. Therefore, the first few rays and the membrane are darker than the rest, as in many cyprinids. In most *Phoxinus* species, breeding individuals show slightly darker pectoral fin than nonbreeding ones (TS 26[0]). However, in *P. neogaeus*, the pectoral fin is much darker (TS 26[1]) in breeding males than in nonbreeding males (Fig.30A, B). No variation of the color pattern is present in nonnuptial individuals among the species of *Phoxinus*.

All rays of the pelvic fin and interradial membranes between rays bear melanophores. The first ray is darker than rest of the fin. No significant variation in color pattern of the pelvic fin is present in the genus.

Melanophores are present on the dorsal fin (Fig.30C, D), and higher density of the melanophores is present on the first ray than on other rays. The highest density of melanophores is at the fin's base. In *P. cumberlandensis* and *tennesseensis*, the melanophores are not much more concentrated at the base than rest of the dorsal fin (TS 27[0]; Fig.30D). In other species of the genus, the melanophores are much more concentrated at the base than rest of the dorsal fin, thus a very dark region is present at the base of the dorsal fin (TS 27[1]; Fig.30C). The latter condition is not present in the outgroups.

All anal fin rays and the interradial membrane bear malanophores. The first fin ray (unbranched) has slightly more melanophores than the remaining rays. No dark patch is formed at base of the anal fin. No significant variation in anal fin pigmentation is present among the species of *Phoxinus*.

The caudal fin, like the dorsal one, bears melanophores on entire fin. More melanophores are present at the dorsal and ventral part of the caudal fin than the middle of the fin in most species of *Phoxinus*. A round blotch is present at the base of the fin (TS 28[0]) in *P. phoxinus, tennesseensis, erythrogaster, eos*, and *neogaeus*; the blotch is absent in other species of *Phoxinus* (TS 28[1]). In the outgroups, the caudal fin bears a round black blotch at its base.

Intestine and Gas Bladder

Intestine (Figs 31A-G, 32A-D)

The intestine of cyprinids is relatively simple without a stomach and pyloric appendages (caeca) (Harder 1975). However, in some species of cyprinids the most anterior section of the intestine is enlarged, forming a pseudogaster. The length and coiling patterns of the intestine show a lot of variation in cyprinids. Kafuku (1958) studied the intestines of cyprinids and defined six looping types in the family, i.e., (in order of increasing complexity) S-, *Zacco*-, Gobionidae-, *Cyprinus*-, *Ctenopharyngodon*-, and Acheilognathinae-types. Harder (1975) added another, the Screw-type, to the list. The morphology of the intestine is widely used in the identification of species and genera in Cyprinidae (e.g., Cross 1967, Cross & Collins 1975).

The intestine in *Phoxinus* is coiled and the looping pattern varies from very simple patterns to complicated ones. The intestine of the genus can be classified into the *Cyprinus*-type of Kafuku (1958) with different degrees of modifications (simpler or more complicated). The species of *Phoxinus* share the following two characteristics in the coiling pattern of the intestine (Figs.31A-G, 32A-D):

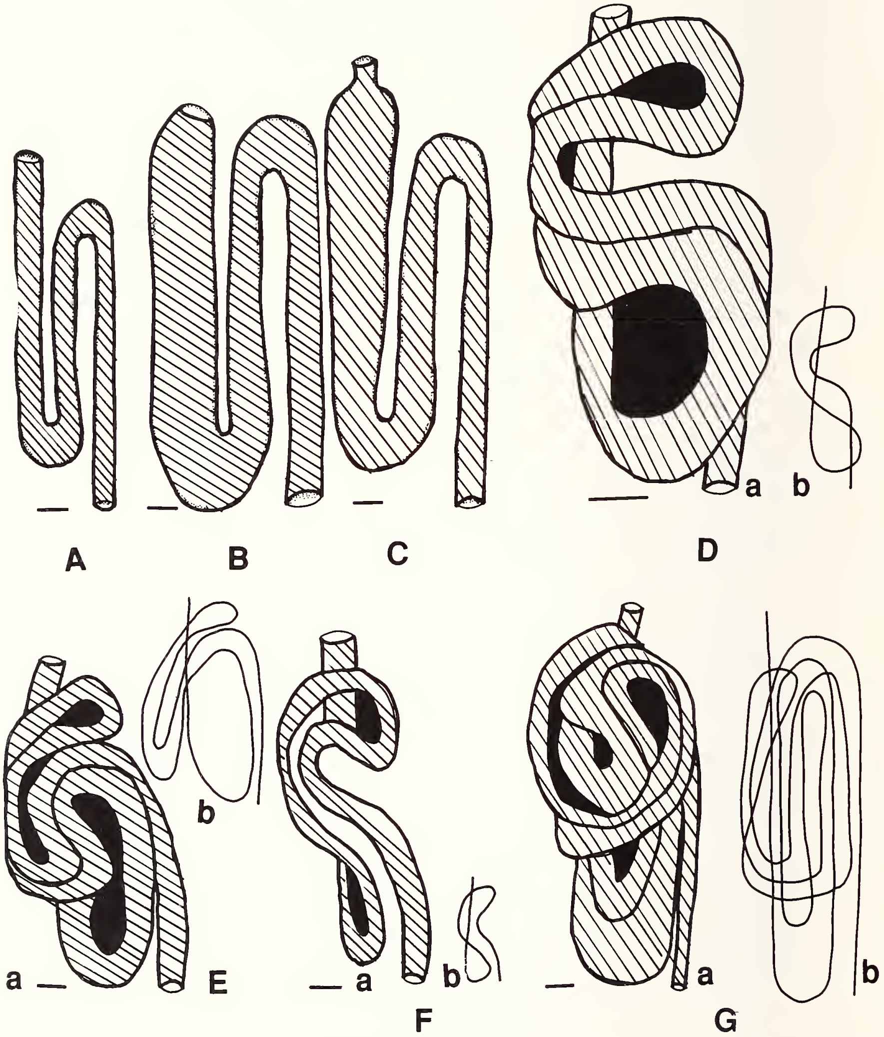

Fig.31: Dorsal view of intestine (a) and its diagrammatic model (b) of *Phoxinus*. A: *P. neogaeus* (KU 14254, 51.8 mm SL); B: *P. issykkulensis* (P-10696, 42.4 mm SL); C: *P. phoxinus* (KU 22853, 56.4 mm SL); D: *P. cumberlandensis* (ANSP 138365, 33.0 mm SL); E: *P. eos* (KU 4578, 41.8 mm SL); F: *P. cumberlandensis* (ANSP 138365, 24 mm SL); G: *P. cumberlandensis* (UT 44.3096, 51.3 mm SL). Scale bars = 1 mm.

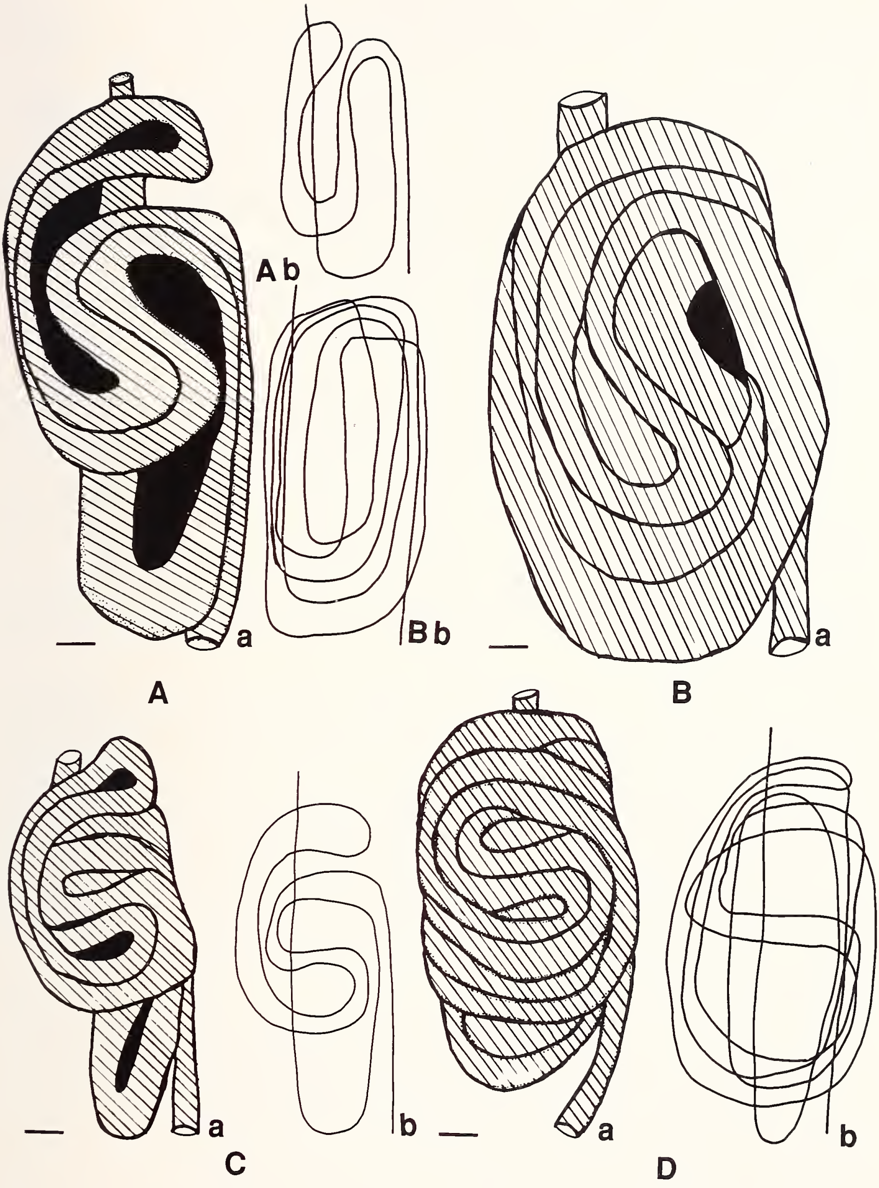

Fig.32: Dorsal view of intestine (a) and diagrammatic model (b) of some species of *Phoxinus*. A: *P. erythrogaster* (KU 3895, 63.1 mm SL); B: *P. tennesseensis* (UT 44.5274, 55.7 mm SL); C: *P. tennesseensis* (ANSP 134735, 47.6 mm SL); D: *P. oreas* (DU field no. B58-3, 59.9 mm SL). Scale bars = 1 mm.

1. The first loop is formed in the following way: the anterior portion of the intestine runs caudally at the left of the body, then turns right, forward then caudally to form the second loop.
2. The beginning of the intestine is located on the left side of the body, whereas the posterior end of the intestine is on the right side of the body.

Significant interspecific variation in *Phoxinus* occurs in the coiling pattern of the intestine. Based on the length, the number and the complexity of loops of the intestine, four types, i.e., *phoxinus-*, *eos-*, *cumberlandensis*-type, and *oreas*-type, can be defined in the genus.

P. phoxinus-type: The intestine is short; its length is shorter than, or equal to standard length of the individual; only 1.5 loops are formed. This type is present in *P. phoxinus, brachyurus, issykkulensis*, and *neogaeus* (Figs.31A-C).

P. eos-type: The intestine is longer than the *phoxinus*-type; its length is about 200% of standard length. Three loops are present. The third loop encloses most of the first one. This type is present in *P. erythrogaster, eos*, and *tennesseensis* (Figs.31E, 32A, C).

P. cumberlandensis-type: The intestine is longer than the *eos*-type. Its length is 230% of the standard length. The coiling pattern of the intestine is more complicated; six loops are present. This type is present in *P. cumberlandensis* only (Fig.31G).

P. oreas-type: This is the most complicated one in the four types. About 10 loops are formed. Its length is about 180% of the standard length. This type is present in *P. oreas* only (Fig.32D).

Ontogenetically, the younger individuals have simpler coiling patterns than the adults in the *Phoxinus* species with a coiled intestine. For instance, *P. cumberlandensis* which bears *cumberlandensis*-type in adults has two loops with a simple coiling in a 24 mm SL individual; two loops with more complicated looping are present in a 33mm SL individual; more complicated looping and more loops are present in a 51.3 mm SL specimen (Fig.31D, F, G). In the outgroups, the intestine is short and the coiling type is simple, similar to the *Phoxinus*-type. Therefore, I hypothesize the polarity of this transformation series is from simple pattern to complicated ones, i.e., *P. phoxinus*-type (TS 29[0]) → *P. eos*-type (TS 29[1]) → *P. cumberlandensis*-type (TS 29[2]) → *P. oreas*-type (TS29[3]).

Gas bladder (Figs.33A-B; 34A-H)

The gas bladder (air-bladder, swim bladder) in cyprinids consists of two chambers (anterior and posterior ones) and a constriction (or isthmus – Harder 1975) between the two chambers[1]. A pneumatic duct (*tractus pneumaticus*) originates from the dorsal wall of the esophagus and connects with the posterior chamber or with the constriction at its posterior end.

The anterior chamber in *Phoxinus* is shorter than the posterior one. The anterior end of the anterior chamber is slightly broader than its posterior part. The posterior chamber is

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[1]) However, three chambers of the gas bladder are also found in some genera of Cyprinidae (e.g., *Megalobrama, Erythroculter*, see Yi & Wu 1964).

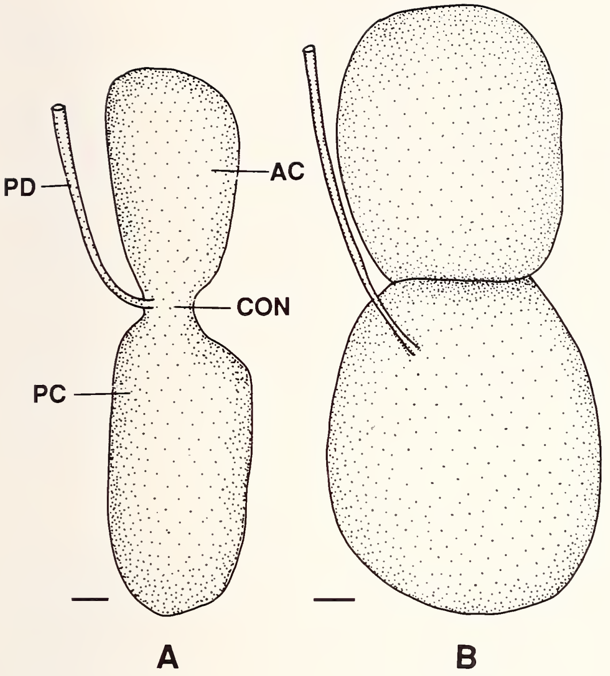

Fig.33: Dorsal view of gas bladder of (A) *Phoxinus erythrogaster* (KU 3895, 63.1 mm SL) and (B) *P. issykkulensis* (P-10696, 42.4 mm SL). Scale bars = 1 mm.

a long tube-like structure; its anterior portion is not broader than its posterior portion in some species of *Phoxinus*.

Morphological variation of the gas bladder among the species of *Phoxinus* is found in the shape of anterior and posterior chambers, the relative length of the two chambers, the length of the constriction, and the position where the pneumatic duct connects with the gas bladder.

The gas bladder is long and slender in *P. phoxinus* (TS 30[1]; Fig.34B). The gas bladder is very short and broad in *P. issykkulensis* (TS 30[2]; Fig.33B). Other species are similar to the outgroups in having a gas bladder that is broader and shorter than that in *P. phoxinus*, but narrower and more slender than that in *P. issykkulensis* (TS 30[0]).

The relative length between the posterior and anterior chambers also varies. Three different conditions can be recognized in the relative length of the two chambers.

(1) The anterior chamber is about 70% of the posterior one in length (TS 31[0]; Fig.34D). In *P. neogaeus* and *erythrogaster*, the anterior chamber is about 75% of the posterior chamber. In *P. tennesseensis, oreas, cumberlandensis, brachyurus*, and *eos*, the anterior chamber is about 70% in length of the posterior one.

(2) In *P. phoxinus*, the anterior chamber is less than 50% in length of the posterior one (TS 31[1]; Fig.34B).

(3) In *P. issykkulensis*, the anterior chamber is almost equal in length to the posterior one (TS 31[2]; Fig.33B).

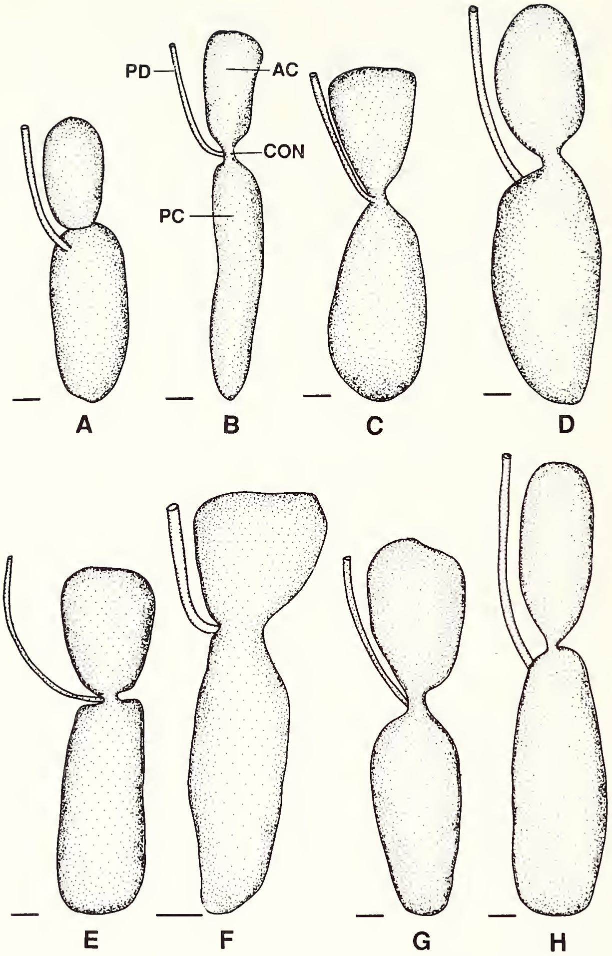

Fig.34: Dorsal view of gas bladder of *Phoxinus*. A: *P. eos* (KU 4578, 41.8 mm SL); B: *P. phoxinus* (KU 22853, 56.3 mm SL); C: *P. oreas* (DU field no. B-58-3, 59.9 mm SL); D: *P. tennesseensis* (UT 5274, 50.0 mm SL); E: *P. cumberlandensis* (UT 44.3096, 51.3 mm SL); F: *P. cumberlandensis* (ANSP 138356, 33 mm SL); G: *P. neogaeus* (KU 14254, 51.8 mm SL); H: *P. brachyurus* (MCZ 3006, 75.9 mm SL). Scale bars = 1 mm.

The condition in *P. erythrogaster* is plesiomorphic because it is similar to that in the outgroups, and other conditions are proposed to be apomorphic.

The constriction of the gas bladder is long and narrow in *P. phoxinus* and *neogaeus* (TS 32[2]; Fig.34B, G). It is shorter and broader in *P. oreas, brachyurus, erythrogaster, cumberlandensis*, and *tennesseensis* (TS32[1]; Fig.34C). It is very short, almost absent in *P. issykkulensis* and *eos* (TS 32[0]; Figs.33B, 34A). A very short constriction is present in the outgroups, and also in young specimens of *Phoxinus* species. Length of the constriction increases ontogenetically, as shown by *P. cumberlandensis* (Fig.34E, F). The polarity of this transformation series (TS 32) is therefore interpreted as very short [0] → short [1] → long [2].

The pneumatic duct connects to the anterior portion of the posterior chamber in *P. eos, brachyurus, issykkulensis*, and *tennesseensis* (TS 33[1]; Fig.34A). In other species of *Pho-*

xinus and in the outgroups, the duct connects to the constriction of the gas bladder (TS 33[0]; Fig.34C).

Peritoneum

The peritoneum is an epithelial membrane lining the interior of the abdominal cavity which contains the intestine and other organs. The peritoneum in *Phoxinus* varies in color. In *P. phoxinus, issykkulensis*, and *brachyurus*, the peritoneum is silver with few melanophores (TS 34[0]; Fig.35A). In all other species of *Phoxinus* (all are North American species), the peritoneum is dark with numerous melanophores (TS 34[1]).

As a rule of thumb, at least in North American cyprinids, species with a long intestine always have a black peritoneum (e.g., *P. erythrogaster*); and species with a short intestine have a silver peritoneum, except that a few species which bear short intestine have a dark peritoneum. *P. neogaeus* is one of the exceptions. I treat a short intestine with silver peritoneum as the plesiomorphic condition.

OSTEOLOGY

For each bone, the general morphology and its relationships with its neighbor elements are described. Then a comparison on shape and size of the bone among the species of *Phoxinus* and the outgroups are conducted, followed by a discussion on the phylogenetic significance and the polarity of the transformation series in the genus *Phoxinus*.

Following Harder (1975), I divide the skeletal system of *Phoxinus* into four sections, i.e., neurocranium, viscerocranium, vertebral column, and appendages.

Neurocranium

Similar to most cyprinids (e.g., Ramaswami 1955a, b), the dorsal aspect of the neurocranium of *Phoxinus* is relatively flat; the posterior portion of the neurocranium is slightly higher and wider than the anterior one. The neurocranium can be divided into five regions, i.e., the ethmoidal, orbital, otic, occipital, and basicranial region.

Ethmoidal Region

This is the most anterior region of the neurocranium. The bones in this region are composed of dermal (e.g., nasal bone) and endochondral (e.g., mesethmoid) elements. Bones included in the region are kinethmoid, supraethmoid, mesethmoid, lateral ethmoid, and preethmoid (cartilage). Among them, the kinethmoid, supraethmoid, and mesethmoid are single, whereas the others are paired elements. The vomer belongs to the basicranial region.

In *Phoxinus*, the supraethmoid, lateral ethmoid, kinethmoid, and preethmoid may be observed in the dorsal view of the ethmoidal region. The lateral ethmoid, preethmoid, and kinethmoid are visible in the ventral view. The mesethmoid can be observed dorsally only after the supraethmoid is removed, or posteriorly after removing the orbital region. The olfactory organ is placed in the olfactory capsule which lies on the ethmoidal region.

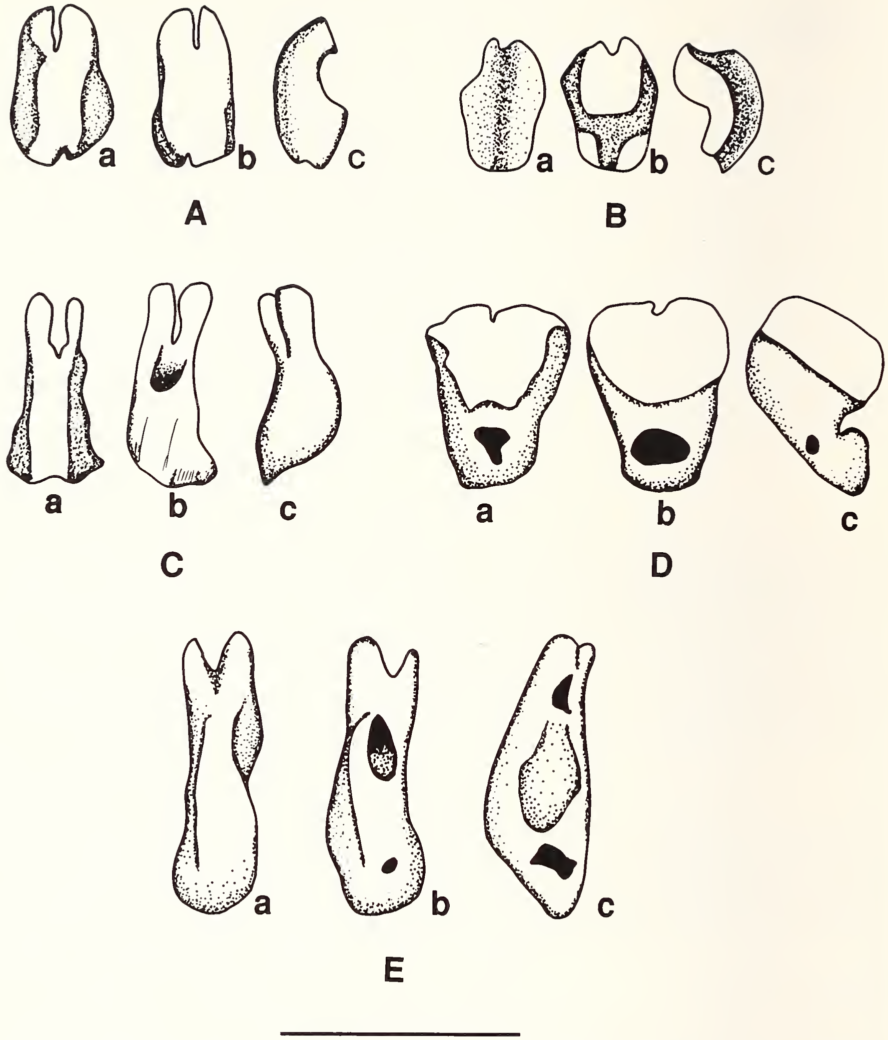

Fig.35: Kinethmoid of *Phoxinus* (a: anterior view; b: posterior view; c; lateral view). A: *P. erythrogaster* (KU 5773, 51.5 mm SL); B: *P. eos* (KU 12255, 43.0 mm SL); C: *P. cumberlandensis* (KU 18934, 52.0 mm SL); D: *P. neogaeus* (KU 8521; 53.0 mm SL); E: *P. phoxinus* (CNUC uncat., 76.0 mm SL). Scale bars = 1 mm.

Kinethmoid (Fig.35A-E). This small median endochondral bone is located at the anterior end of the neurocranium. This bone is bar-like, with numerous modifications on its dorsal and lateral aspects in cyprinids (Ramaswami 1955a, b). Via ligaments, the bone joins with the supraethmoid posteriorly, and maxilla and premaxilla laterally in cyprinids (Ramaswami 1955a, b, Harder 1975, Mayden 1989).

In *Phoxinus*, the kinethmoid-supraethmoidal ligament connects with posterodorsal side of the kinethmoid and with anterior side of the supraethmoid. The kinethmoid-maxillary ligament connects with the dorsolateral side of the kinethmoid and with a anterior process of the maxilla. The kinethmoid-premaxillary ligament connects with the anterior portion of the kinethmoid and with anterior side of the premaxilla. The position of the kinethmoid is flexible. When mouth opens, the kinethmoid moves ventroanteriorly; while mouth is closed, the kinethmoid moves back posterodorsally.

The kinethmoid is slender and crescent in shape. In *P. phoxinus, erythrogaster, oreas, issykkulensis, tennesseensis*, and *cumberlandensis*, the distance between its ventral and dorsal margins is longer than the width between its two lateral margins (left and right margins) (TS 35[1]) (Fig.35A, C, E). In *P. neogaeus, brachyurus*, and *eos*, however, the bone is short and robust, its dorsal portion is wider than its ventral portion (TS 35[0]; Fig.35B, D).

The dorsal edge of the kinethmoid is forked or notched. In *P. cumberlandensis* and *erythrogaster*, its anterior dorsal edge is deeply forked (TS 36[1]; Fig.35A, C); the fork is deep and narrow, the depth of the fork is about one third of the bone length (dorsal-ventral). In *P. brachyurus, phoxinus, neogaeus, eos, tennesseensis, issykkulensis*, and *oreas*, the anterior dorsal margin of the bone is shallowly notched, the notch is wider and about one-sixth of the bone length in depth (TS 36[0]; Fig.35B, D, E). In the outgroups, the dorsal margin of the kinethmoid is shallowly notched. Based on the outgroup comparison, a shallowly notched dorsal margin of the kinethmoid is therefore interpreted as plesiomorphic, the deeply forked dorsal margin of the bone as apomorphic condition.

Posteriorly, the kinethmoid is concave at its middle portion in most species of *Phoxinus* (TS 37[0]) except *P. brachyurus* and *eos*. In the latter two species, the kinethmoid is not concave but slightly convex at its middle portion of the posterior side (TS 37[1]). A foramen from the anterior side to the posterior side of the bone is present in *P. neogaeus* and *phoxinus* (TS 38[1]; Fig.35D, E). The foramen is not observed in all other *Phoxinus* species (TS 38[0]) and in the outgroups.

A notch is present at the ventral edge of the kinethmoid in *P. erythrogaster* (TS 39[1]; Fig.35A). The notch is not observed in other species of *Phoxinus* and in the outgroups (TS 39[0]; Fig.35B-E).

Supraethmoid (Fig.36A-E). In cyprinids, the supraethmoid is a single dermal bone located in front of the paired frontals. Its ventral side is sutured to the dorsal side of the mesethmoid. The shape of the supraethmoid is variable in minnows; it might be narrow (e.g., *Barilius*), or "extending so much that it may be visible on the ventral aspect of the skull" (e.g., *Labeo*) (Ramaswami 1955a). In some genera of the family Cyprinidae (e.g., *Aristichthys*), there is a small median fontanelle between the supraethmoid and the frontal (Ramaswami 1955a).

In *Phoxinus*, the supraethmoid is thin and slightly concave at the middle portion of its dorsal aspect, and more or less rectangular-shaped. The lateral portion of the supraethmoid roofs the anterior part of the olfactory capsule. Both the anterolateral and the anterior margins are concave in all *Phoxinus* species, and the posterior margin is concave in most species of *Phoxinus*.

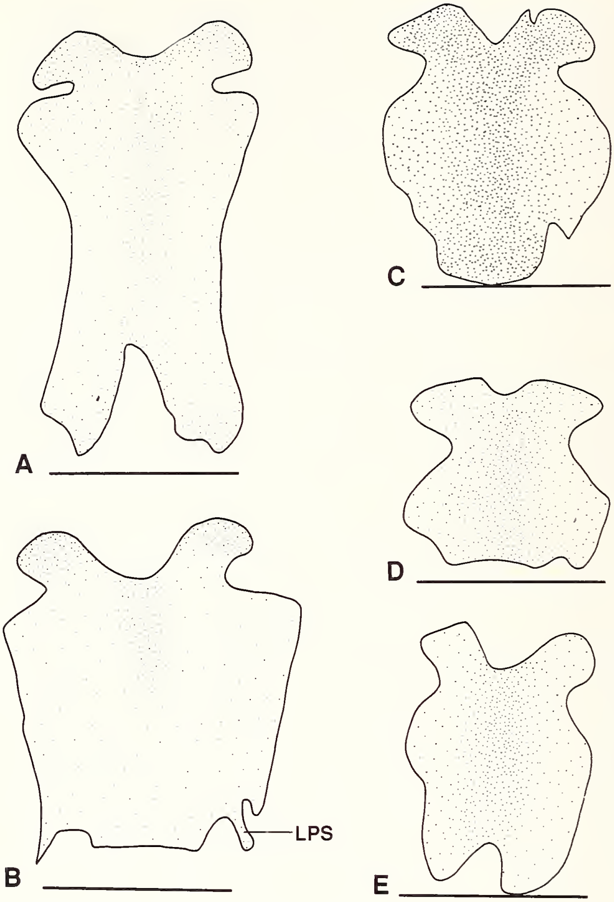

Fig.36: Dorsal view of the supraethmoid of *Phoxinus*. A: *P. phoxinus* (CNUC uncat., 76.0 mm TL); B: *P. neogaeus* (KU 8521, 53.0 mm SL); C: *P. erythrogaster* (KU 5773, 51.5 mm SL); D: *P. oreas* (KU 3259, 55.0 mm SL); E: *P. eos* (KU12255, 43.0 mm SL). Scale bars = 1 mm.

Variation of the supraethmoid among *Phoxinus* species affects its general shape and shape of the lateral and posterior margins. The supraethmoid is short and relatively broad in *P. neogaeus, oreas, eos, erythrogaster*, and *tennesseensis* (TS 40[1]); whereas it is elongated, relatively narrow, and slender in *P. phoxinus, brachyurus, issykkulensis*, and *cumberlandensis* (TS 40[0]). The middle of the lateral margin of the supraethmoid is convex and forms a small process in *P. oreas, eos, brachyurus*, and *erythrogaster* (TS 41[0]; Fig.36C, D); the lateral margin is straight in *P. tennesseensis* and *neogaeus*; it is concave and forms a waist-like structure in *P. cumberlandensis, issykkulensis*, and *phoxinus* (TS 41[1]; Fig.36A, E). The concavity at the lateral margin is shallow in *P. phoxinus*; it is deeper but narrow in *P. cumberlandensis*. The posterior margin of the supraethmoid is slightly concave in *P. oreas*; deeply concave in *P. phoxinus, brachyurus, eos*, and *issykkulensis* (TS 42[0]); it is not concave in other species (TS 42[1]), among them the posterior margin of the bone is convex in *P. erythrogaster, tennesseensis*, and *neogaeus*; it is almost straight in *P. cumberlandensis*. Mahy (1975b) stated that the posterior margin of the supraethmoid is concave in *P. neogaeus*. However, my study showed the posterior margin is not concave but bears a lateroposterior process at the posterolateral portion of the bone in *P. neogaeus* (TS 43[1]). The processes were not observed in other species of *Phoxinus* (TS 43[0]).

In the outgroups, the supraethmoid is elongated and relatively narrow; the middle region of the lateral margin is convex, and the posterior margin is deeply concave.

Nasal bone (Fig.37A-G). In cyprinids, the nasal bone is a paired dermal element without direct connection with any other bones. It is placed lateral to the supraethmoid, and anterolateral to the frontal bone and forms part of the dorsal cover of the olfactory capsule. The bone bears part of the supraorbital canal. In *Phoxinus*, the nasal bone is narrow and elongated. The supraorbital canal runs through the middle of the bone in *P. brachyurus, oreas, phoxinus, tennesseensis, erythrogaster, neogaeus*, and *cumberlandensis* (TS 44[0]; Fig.37A-B); whereas, in *P. issykkulensis* and *eos*, the nasal bone is relatively broad and short and expands mesially; the nasal portion of the supraorbital canal runs on the lateral part of the nasal bone (TS 44[1]; Fig.37G). In *P. brachyurus* and *cumberlandensis*, the nasal portion of the supraorbital canal is broken at its dorsal side (TS 45[1]; Fig.37A); in other species, the nasal portion of the supraorbital canal is complete (not interrupted) (TS 45[0]; Fig.37B). The relative position of the nasal bone to its neighbor bones also varies among the *Phoxinus* species. In *P. neogaeus, cumberlandensis*, and *issykkulensis*, the entire nasal bone is over the lateral ethmoid (TS 46[1]). In *P. brachyurus, oreas, erythrogaster, tennesseensis, eos*, and *phoxinus*, the nasal bone's posterior portion is placed over the lateral ethmoid, while its anterior portion is positioned over the mesethmoid (TS 46[0]; Fig.37A).

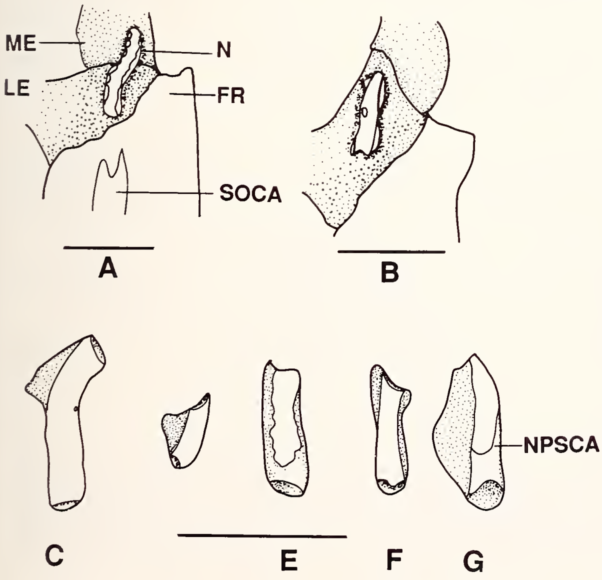

Fig.37: Dorsal view of mesethmoid, lateral ethmoid, frontal, and nasal bones (C-G showing nasal bone only) in *Phoxinus*. A: *P. brachyurus* (MCZ 3006, 75.9 mm SL); B: *P. neogaeus* (KU 8521, 53.0 mm SL); C: *P. tennesseensis* (UT 44.5274, 50.0 mm SL); D: *P. issykkulensis* (P-10696, 42.4 mm SL); E: *P. cumberlandensis* (KU 18934, 52.0 mm SL); F: *P. phoxinus* (KU 22856, 58.0 mm TL); G: *P. eos* (KU 12255, 33.0 mm TL). Scale bars = 1 mm.

In the outgroups, the nasal bone is narrow and elongated, and located over the mesethmoid and lateral ethmoid; the nasal portion of the supraorbital canal is not interrupted.

Preethmoid (Fig.38A, B). In cyprinids, the paired preethmoid is located between the anteroventral side of the mesethmoid and anterolateral side of the vomer. Ramaswami (1955a) stated that *Phoxinus* lacks the preethmoid. This is not the case in the specimens of *Phoxinus* I studied. All species of *Phoxinus* have the preethmoid.

In *Phoxinus*, the preethmoid is semi-spherical in shape. Its position in the skull is similar to that in other cyprinids. The variations of the preethmoid among *Phoxinus* species is in its relative size. The preethmoid is well-developed and large in *P. phoxinus* (TS 47[1]). It is smaller, not well-developed in other species of *Phoxinus* and in the outgroups (TS 47[0]).

Mesethmoid (Figs.38A-B, 39A-B). In cyprinids, the mesethmoid is an endochondral single bone resting on a cartilage (planum ethmoidale) on the vomer, and located at the ventral side of the supraethmoid (Mayden 1989). In *Phoxinus*, the planum ethmoidale is observed in a 33 mm standard length specimen of *P. eos* (Fig.38A). The cartilage is reduced or absent in larger specimens. Dorsally and anteriorly, the mesethmoid shares sutures with the posterior side of the supraethmoid (Fig.38A-B). The mesethmoid sutures with the lateral ethmoid posteriorly.

The mesethmoid is irregular in shape. Anterolaterally, the bone bears two foramina for nerves (Fig.38A-B). Anteriorly, the mesethmoid is concave; the anterior surface of the mesethmoid sutures with the posterior surface of the supraethmoid. Ventrally, the mesethmoid bears one or two conea (Gasowska 1979), the anterior and posterior ones, which are concave and position at the ventral side of the mesethmoid (Fig.39A-B).

Variation in the mesethmoid of *Phoxinus* occurs mainly at its ventral aspect. In *P. phoxinus*, *neogaeus*, and *eos*, the ventral side of the bone is broad and relatively short (TS 48[1]) and bears two conea (TS 49[0]; Fig.39B). In these three species, the anterior conus is broad, short, and surrounded by the arch-like posterior one. In other species of *Phoxinus*, the bone is relatively elongated and narrow (TS 48[0]), only one conus is present (TS 49[1]).

In the outgroups, the ventral side of the mesethmoid is narrow and relatively elongated, but bears two conea. However, the relationships between the two conea in the outgroups

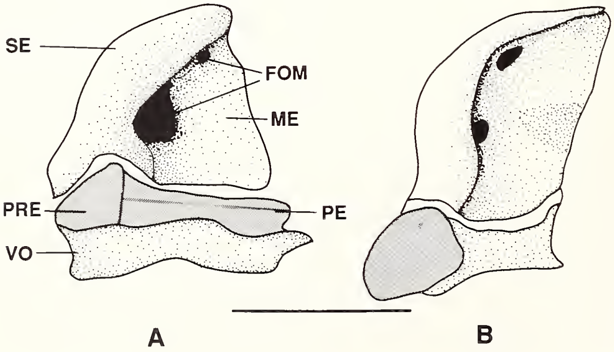

Fig.38: Lateral view of ethmoidal region of (A) *Phoxinus eos* (KU 12255, 33.0 mm SL), and (B) *P. phoxinus* (KU 22856, 58.0 mm SL). Scale bar = 1 mm.

is slightly different from that in *Phoxinus*. In the outgroups, the posterior conus is broad, short, and located posteriorly to the anterior conus.

Lateral Ethmoid (Fig.39C-D). In cyprinids, the lateral ethmoid is located at the anterolateral side of the neurocranium.

Ventrally, the lateral ethmoid sutures with the dorsal aspect of the vomer and of the anterolateral portion of the parasphenoid. The lateral ethmoid sutures posteriorly with the dorsal aspect of the anterior portion of the parasphenoid and the anterior portion of the orbitosphenoid, anteriorly with the mesethmoid and supraethmoid, and dorsally with the ventral side of the frontals. The left and right lateral ethmoids are separated by the parasphenoid and the mesethmoid. The anterior portion of the lateral ethmoid forms part of the bottom of the nasal capsule; the posterior portion of the bone forms the anterior portion of the orbital capsule and the dorsal side of the anterior myodome, and the median portion of the lateral ethmoid forms part of the lateral wall of the braincase. Ventrally, the

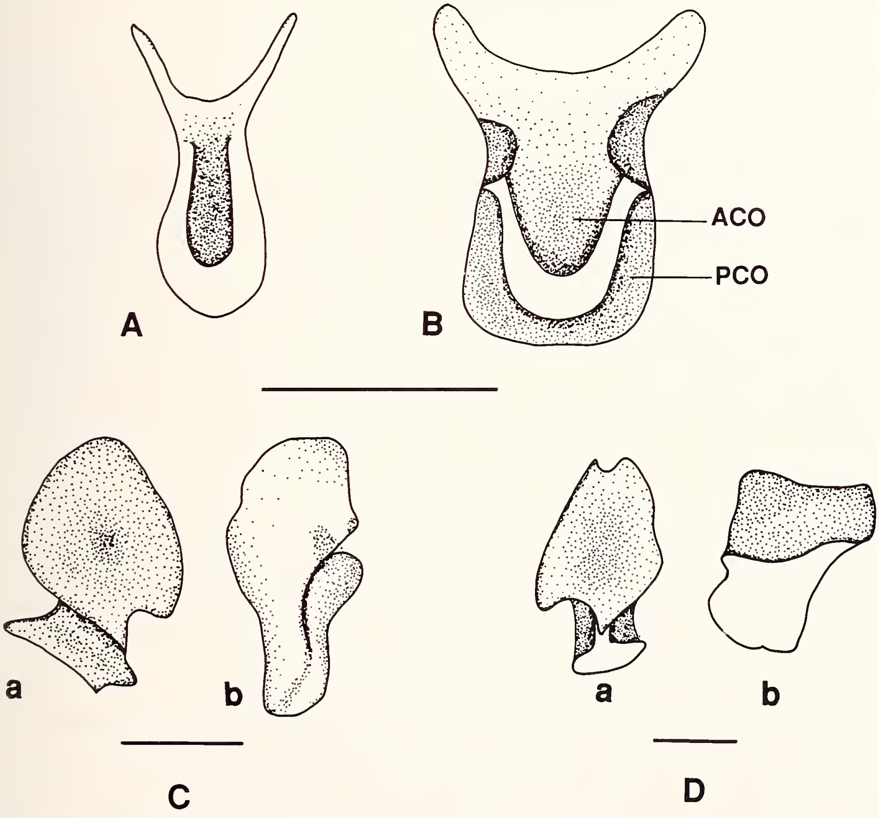

Fig.39: Ventral view of mesethmoid (A-B), and medial (a) and ventral (b) view of lateral ethmoid (C-D) of *Phoxinus*. A: *P. oreas* (KU 3259, 55.0 mm SL); B: *P. neogaeus* (KU 8521, 53.0 mm SL); C: *P. phoxinus* (CNUC uncat., 76.0 mm TL); D: *P. cumberlandensis* (KU 18934; 52.0 mm SL). Scale bars = 1 mm.

lateral ethmoid expands forming a triangular-shaped portion. Posteriorly, the lateral ethmoid is triangular-shaped. Anteriorly, the lateral ethmoid is similar to its posterior view in shape. Medially, the medial side of the bone is concave and bears a notch at its ventral margin. The bone has a T-shaped ridge-like appearance dorsally.

Variation of the lateral ethmoid among *Phoxinus* species affects its shape. Ventrally, the anterior and posterior portions are acute in *P. cumberlandensis* and *erythrogaster* (TS 50[0]; Fig.39D). In *P. erythrogaster*, the anteroventral portion is elongated and forms a process. The anterior and posterior portions of the ventral aspect are blunt in other species of *Phoxinus* (TS 50[1]; Fig.39C).

The concave medial side bears a notch at its dorsal margin in *P. tennesseensis* and *cumberlandensis* (TS 51[1]) (Fig.39D); the notch is not present in other species of *Phoxinus* (TS 51[0]; Fig.39C).

In the outgroups, the anterior and posterior portions of the ventral aspect of the lateral ethmoid are acute; no notch is present at the dorsal margin of the medial aspect of the lateral ethmoid.

Orbital Region

Located posteriorly to the ethmoidal region, the orbital region consists of orbitosphenoid, pterosphenoid, frontal, supraorbital, and infraorbital bones.

Frontal (Figs 40A-F). In cyprinids, the frontal is the largest bone in the neurocranium (but in *Aristichthys* the frontal is a small bone – Ramaswami 1955a), and forms the anterodorsal cover of braincase. Shape of the frontal varies from short and broad (e.g., *Rhodeus*) to very slender and elongated (e.g., *Elopichthys bambusa, Luciobrama macrocephalus* – Howes 1978, Chen 1987c). Dorsally, it shares a suture with the supraethmoid anteriorly, lateral ethmoid anterolaterally, sphenotic posterolaterally, and parietal posteriorly. In some cyprinids, there is a small fontanel between the anterior margin of the frontal and the posterior margin of the supraethmoid (e.g., species of *Aristichthys*) (Ramaswami 1955a). The left and right frontals meet one another at their mesial margins with slight overlap. Ventrally, the frontal meets the lateral ethmoid anteriorly, orbitosphenoid and pterosphenoid laterally. Anteriorly, the frontal roofs the posterior part of the olfactory capsule.

In *Phoxinus*, frontal sutures with other bones similar to that in other cyprinids. The fontanel between frontal and supraethmoid is absent in the genus. The frontal is a rectangular-shaped bone with a posterolateral process at posterior portion of the lateral margin and an anterior process at its anterior margin. The posterior margin of the posterolateral process sutures with the anterior margin of the sphenotic. Shape of the posterolateral process varies among the species of *Phoxinus*. The posterolateral process is sharp and elongated in *P. neogaeus, issykkulensis, brachyurus*, and *phoxinus* (TS 52[1]); the process is relatively short and broad in other species of *Phoxinus* (TS 52[0]) and in the outgroups. Thus the elongated and sharp posterolateral process is proposed as an apomorphic condition, and the short and broad one a plesiomorphic condition.

The frontal bears the supraorbital canal in *Phoxinus*. The supraorbital canal might be continuous or interrupted. On the ventral side of the frontal bone in *Phoxinus* three concavi-

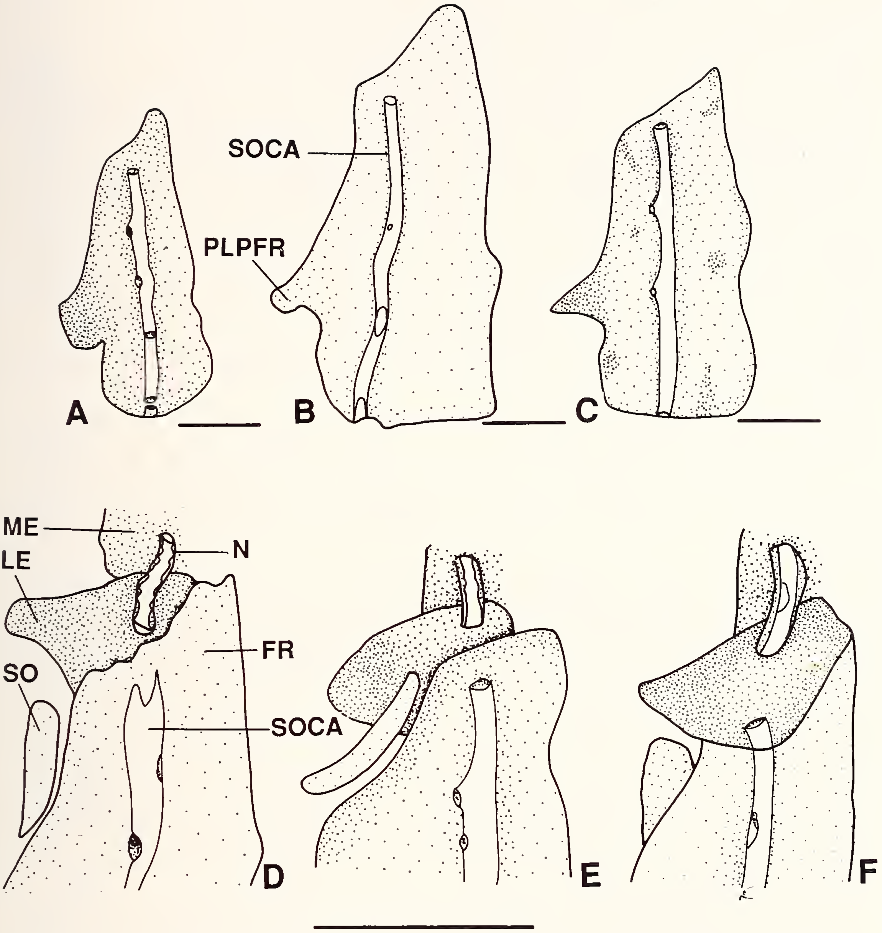

Fig.40: Dorsal view of the frontal bone (A-C), and supraorbital, lateral ethmoid, mesethmoid, frontal, and nasal bones (D-F) of *Phoxinus*. A: *P. cumberlandensis* (KU 18934, 52.0 mm SL); B: *P. erythrogaster* (KU 5773; 51.5 mm SL); C: *P. phoxinus* (CNUC uncat., 76.0 mm TL); D: *P. oreas* (KU 3259, 55.0 mm SL); E: *P. phoxinus* (KU 22856, 58.0 mm SL); F: *P. tennesseensis* (UT 44.5274, 50.0 mm SL). Scale bars = 1 mm.

ties are present, including anterolateral, anteromedial, and posterior ones. The anterolateral and anteromedial concavities are separated by a ridge. The posterior concavity is triangular-shaped and separated by a ridge from the anterolateral and anteromedial concavities.

Supraorbital (Fig.40D-F). In cyprinids, this paired bone is flat plate-shaped with variation in size from broad and short (e.g., *Ctenopharyngodon* and *Hypophthalmichthys* – Howes 1981) to slender and elongated (e.g., *Genghis mongolicus* – Howes 1984). The supraorbital bone is placed at anterolateral side of the frontal. The supraorbital sutures with the frontal medially, and might be over the lateral ethmoid anteriorly.

In *Phoxinus*, the supraorbital is a small, elongated crescentic bone. However, it is relatively shorter and broader in *P. oreas* and *tennesseensis* (TS 53[1]; Fig.40F) than that in other species of the genus in which the supraorbital bone is relatively elongated and slender (TS 53[0]; Fig.40D). Its position relative to the supraethmoid, frontal, and lateral ethmoid also varies among the species. In *P. phoxinus, neogaeus*, and *cumberlandensis*, the supraorbital bone is placed forward; almost half of the supraorbital bone is above the lateral ethmoid (TS 54[1]; Fig.40E). In other species of *Phoxinus*, however, the supraorbital is placed more posteriorly; it does not overlap the lateral ethmoid, or only a small portion of the supraorbital bone overlaps the lateral ethmoid (TS 54[0]; Fig.40F).

In the outgroups, the supraorbital bone is elongated and slender; only a small portion of the bone overlaps the lateral ethmoid.

Infraorbital series (Fig.41A-H). Four or five paired plate-like bones are included in the infraorbital series: infraorbitals 1, 2, 3, 4, and 5 (Fig.41A-H). In some species of Cyprinidae, infraorbital 5 is present as two small pieces (e.g., *Luciobrama macrocephalus* – Howes 1978); in some species, however, infraorbital 5 is absent (e.g., *Cyprinella* – Mayden 1989).

In cyprinids, infraorbital 1 (lacrymal) is the largest and the most anterior bone of the infraorbital series. It is located lateral to the vomer, and medial to the maxilla. In *Phoxinus*, infraorbital 1 (Fig.41A-H) does not directly articulate with any other bone dorsally and dorsoposteriorly, but with infraorbital 2 ventroposteriorly. Infraorbital 1 bears a concavity at its anterior margin and a process on its dorsal margin. An infraorbital canal runs through the bone. In *P. phoxinus* infraorbital 1 is relatively short and broad, its anterior and posterior margins bear a well-developed notch (TS 55[1]; Fig.41E). In other species of the genus and in the outgroups, infraorbital 1 is relatively elongated and narrow, both the anterior and posterior margins bear no notch or bears a very shallow notch (TS 55[0]; Fig.41H).

Infraorbital 2 (Fig.41A-H) is an elongated rectangular bone. It articulates with infraorbital 1 anteriorly and infraorbital 3 posteriorly. Its anterior portion is slightly broader than its posterior portion in *Phoxinus*. There is variation of the bone among the species of *Phoxinus*. In *P. cumberlandensis*, infraorbital 2 is short and relatively broad, its length (anterior to posterior) is less than two times of its width (ventral to dorsal), and the anterior portion is equal to the posterior one in width (TS 56[1]; Fig.41B). The condition in other species of *Phoxinus* are similar to the condition in the outgroups. The bone is elongated and slender, with the length about three times of the width; its posterior portion is slightly narrower than its anterior portion (TS 56[0]).

Infraorbital 3 (Fig.41A-H) is the longest among all infraorbital bones, and occupies about half of the total length of the infraorbital series. (However, infraorbital 4 is the longest among the infraorbital bones in some cyprinids, such as *Luciobrama macrocephalus* – Howes 1978, Chen 1987c). It is crescent in shape, and articulates with infraorbital 2 anteriorly, and infraorbital 4 posteriorly. In *P. neogaeus, cumberlandensis, issykkulensis*, and *erythrogaster*, infraorbital 3 is equal in width, i.e., the width of the bone does not change

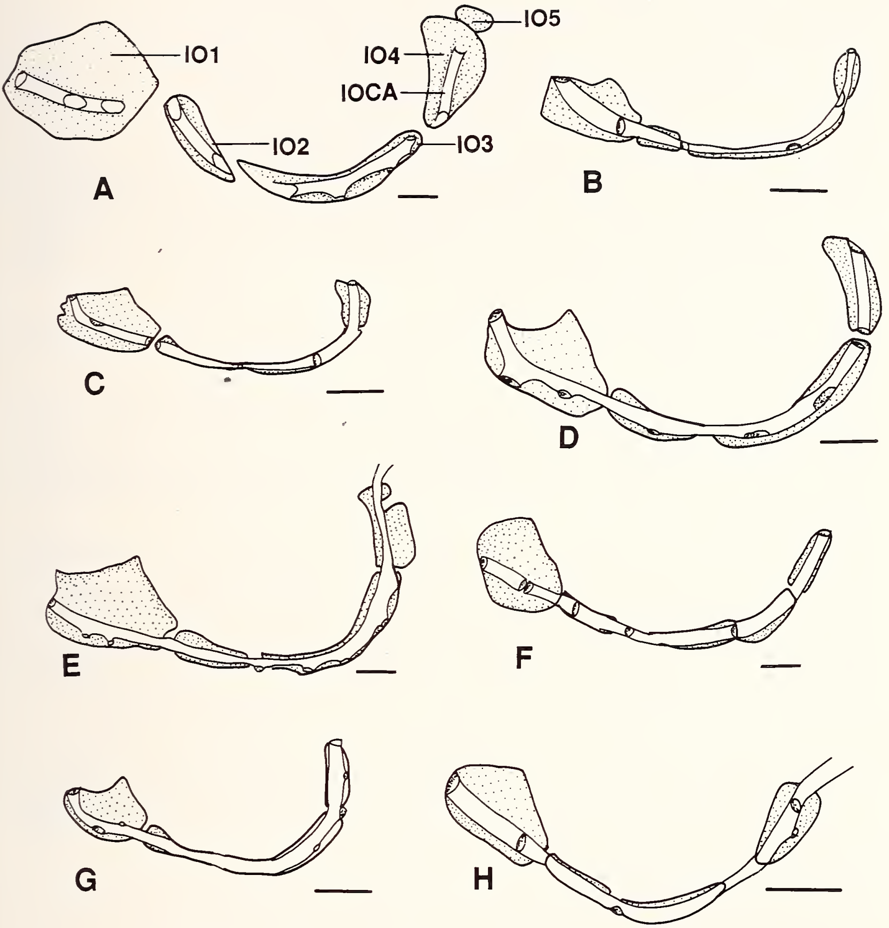

Fig.41: Lateral view of infraorbital bones of *Phoxinus*. A: *P. brachyurus* (MCZ 3006, 75.9 mm SL); B: *P. cumberlandensis* (KU 18934, 52.0 mm SL); C: *P. issykkulensis* (P-10696, 42.4 mm SL); D: *P. erythrogaster* (KU 5773, 62.0 mm SL); E: *P. phoxinus* (CNUC uncat., 76.0 mm TL); F: *P. tennesseensis* (UT 44.5274; 50.0 mm SL); G: *P. oreas* (KU 3259, 52.2 mm SL); H: *P. neogaeus* (KU 8521, 53.o mm SL). Scale bars = 1 mm.

much from its anterior portion to its posterior portion (TS 57[0]; Fig.41B). The posterior portion of the former is much broader than the anterior portion in *P. oreas, phoxinus, tennesseensis, brachyurus*, and *eos* (TS 57[1]; Fig.41E). In *P. tennesseensis* the anterior margin of infraorbital 3 is far from infraorbital 2 (TS 58[1]; Fig.41F); the anterior margin of the former is close to the latter in other species of *Phoxinus* (TS 58[0]; Fig.41H). In the outgroups, infraorbital 3 does not vary much in width along the length, and the anterior margin of the bone is close to the infraorbital 2.

Infraorbital 4 (Fig.41A-H) is the most posterior bone of the infraorbital series in most species of *Phoxinus*, except *P. brachyurus* (see below). Infraorbital 4 meets infraorbital 3 ventrally and has no direct connection with other bones dorsally in most species. It is crescent in shape and varies in the relative size to infraorbital 2 among the *Phoxinus* species. In *P. eos* and *erythrogaster*, infraorbital 4 is slightly shorter than infraorbital 2. In *P. cumberlandensis, issykkulensis*, and *tennesseensis*, it is about the same size as infraorbital 2 (TS 59[0]; Fig.41B). The bone is expanded and much wider than infraorbital 2 in the remaining species of *Phoxinus* (TS 59[1]; Fig.41E). In *P. phoxinus* the bone bears a notch at the dorsal portion of its posterior edge (TS 60[1]; Fig.41E). The notch is absent in other species of *Phoxinus* (TS 60[0]; Fig.41A).

In the outgroups, infraorbital 4 is about same size as the infraorbital 2, and bears no notch at the posterior margin.

Positioned at the dorsal side of infraorbital 4, infraorbital 5 is a small dermal bone and is present in *P. brachyurus* only (TS 61[1]; Fig.41A). The bone is small and irregular-shaped plate-like. It is not observed in the outgroups (TS 61[0]; Fig.41B). Infraorbital 5 articulates with the dorsal margin of infraorbital 4 ventrally, and has no direct connection with other bones on its dorsal side.

Orbitosphenoid (Fig.42A-D). In cyprinids, the orbitosphenoid is a paired chondral bone. The orbitosphenoid is sutured by the lateral ethmoid anteriorly, parasphenoid ventrally, frontal dorsally, and pterosphenoid posteriorly. Gasowska (1979) stated that the orbitosphenoid is a single bone in cyprinids. However, Howes (1978) showed a pair of orbitosphenoids in *Luciobrama macrocephalus*. My study on *Phoxinus* demonstrated that the orbitosphenoid is paired in this genus.

In *Phoxinus*, each orbitosphenoid is a plate-like bone. The ventral portion of the bone is very thin and sutures with the same portion of other orbitosphenoid medially to form the orbital septum. The orbital septum is concave at the middle or dorsal part of its posterior margin, the ventral part of its posterior margin is convex.

The relative position of the ventral part of the posterior margin of the septum (the very thin portion of the orbitosphenoid) to the dorsal portion of the posterior margin of the orbitosphenoids varies among the species of *Phoxinus*. The posterior margin of the septum extends posteriorly beyond the posterior margin of the dorsal portion of the orbitosphenoids in *P. neogaeus*. The septum almost extends to the posterior margin of the dorsal portion of the orbitosphenoids in *P. eos* and *phoxinus* (TS 62[1]); the posterior margin of the septum is far away from the posterior margin of the unfused portion of the orbitosphenoid in other species of *Phoxinus* and in the outgroups (TS 62[0]).

The shape of the posterior edge of the orbital septum varies among the *Phoxinus* species. In *P. cumberlandensis* and *P. erythrogaster*, a process is present on the ventral portion of the posterior margin of the septum (TS 63[1]). This process is not observed in other species of *Phoxinus* and in the outgroups (TS 63[0]).

Pterospenoid (Fig.42A-D, 43A-B). In cyprinids, the pterosphenoid is a paired bone sutured with the orbitosphenoid anteriorly, frontal anterodorsally, sphenoid posterodorsally, prootic posteriorly, and parasphenoid ventrally. In *Phoxinus*, the posterodorsal edge of the

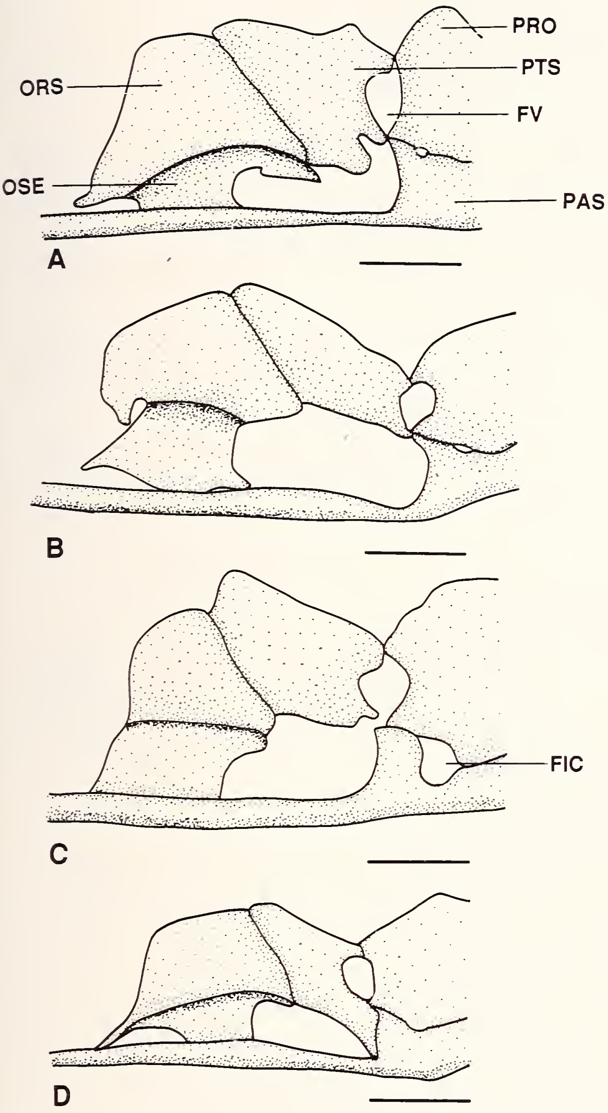

Fig.42: Lateral view of orbitosphenoid, pterosphenoid, prootic, and parasphenoid of *Phoxinus*. A: *P. neogaeus* (KU 8521, SL 53.0 mm); B: *P. erythrogaster* (KU 5773, SL 51.5 mm); C: *P. oreas* (KU 3259, SL 55.0 mmmm); D: *P. eos* (KU 12255, SL 43.0 mm). Scale bars equal 1 mm.

pterosphenoid forms the anterior part of the hyomandibular fossa, and its posterior margin forms the anterior part of the trigeminal foramen.

The pterosphenoid is irregularly shaped in *Phoxinus*. A process is present at its anterior margin in *P. eos, erythrogaster*, and *phoxinus* (TS 64[1]); the process is absent in other species of the genus and in the outgroups (TS 64[0]). The posterior margin of the pterosphenoid bears a notch which forms the anterior part of the trigeminal foramen. The po-

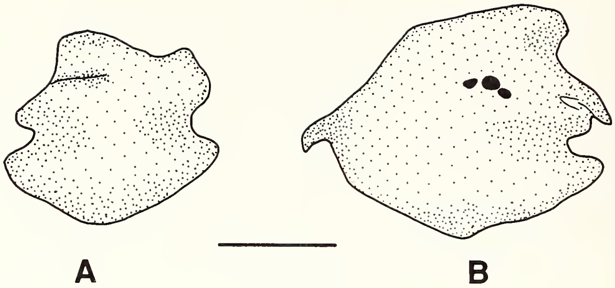

Fig.43: Lateral view of pterosphenoid of (A) *Phoxinus cumberlandensis* (KU 18934, 52.0 mm SL) and (B) *P. phoxinus* (CNUC uncat., 76.0 mm TL). Scale bar = 1 mm.

sterior portion of the bone bears a process in *P. oreas, issykkulensis, tennesseensis, eos, neogaeus, brachyurus, phoxinus*, and in the outgroups (TS 65[0]), although the process is absent in *P. cumberlandensis* and *erythrogaster* (TS 65[1]).

The pterosphenoid's ventroposterior margin sutures with anterior edge of the parasphenoid's ascending wing (Fig.42A-D). Variation in *Phoxinus* is present in the extent of the suture between the pterosphenoid and the ascending wing of the parasphenoid. In *P. neo-*

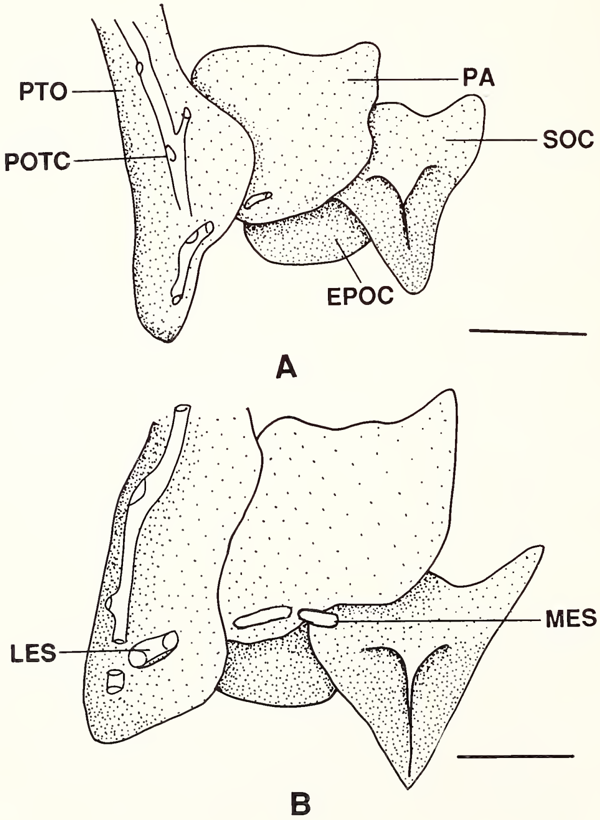

Fig.44: Dorsal view of pterotic, parietal, epioccipital, and supraoccipital (A) *Phoxinus tennesseensis* (UT 44.5274, 50.0 mm SL) and (B) *P. brachyurus* (MCZ 3006, 75.9 mm SL). Scale bars = 1 mm.

gaeus, erythrogaster, brachyurus, eos, and in the outgroups, only a very small portion of the pterosphenoid articulates with the parasphenoid (TS 66[0]). A much larger portion of the pterosphenoid sutures with the wing of the parasphenoid in other species of *Phoxinus* (TS 66[1]).

Otic Region

Located posteriorly to the orbital region, the otic and occipital regions form the otic capsule. Bones in the otic region include parietal, medial extrascapula, sphenotic, prootic, epioccipital, intercalar, pterotic, and lateral extrascapula. All are paired bones.

Parietal and medial extrascapula (Fig.44A-B). In cyprinids, the parietal is a paired dermal bone located at the posterodorsal portion of the neurocranium, and forms the posterodorsal cover of the braincase. The parietal sutures with the frontal anteriorly, sphenotic anterolaterally, pterotic posterolaterally, supraoccipital and epioccipital posteriorly. The left and right parietals suture each other mesially with a small overlap at its middle and posterior portion. Length of the parietal is usually about 30-50% of the frontal length (Howes 1981). A parietal fontanelle exists between the parietal and frontal in some

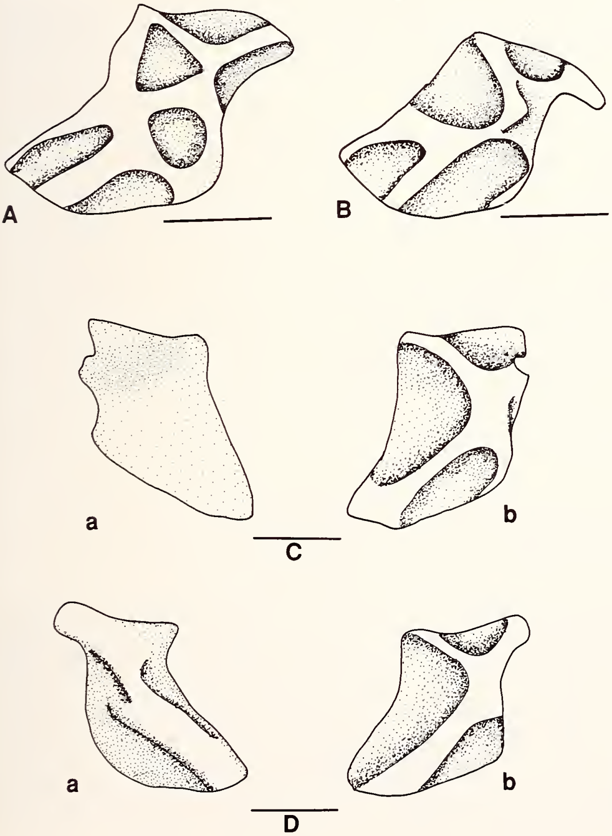

Fig.45: Sphenotic of *Phoxinus*. A: *P. oreas* (KU 3259, SL 55 mm, ventral view); B: *P. eos* (KU12255, 43.0 mm SL, ventral view); C: *P. phoxinus* (CNUC uncat., 76.0 mm TL); D: *P. cumberlandensis* (KU 18934, 52.0 mm SL) (a: dorsal view; b: ventral view). Scale bars = 1 mm.

cyprinids, such as *Cyprinus carpio* (pers. obs.) and some gobions (Ramaswami 1955b). The fontanelle is absent in *Phoxinus*.

In *Phoxinus* the parietal is more or less rectangular plate-like in shape. No variation in shape of the parietal is observed among the *Phoxinus* species.

The medial extrascapula is a small bar-shaped bone carrying the supratemporal canal and is located at the dorsal side of the posterior portion of the parietal. One medial extrascapula is present, partially covering the parietal in *P. neogaeus, brachyurus*, and in the outgroups (TS 67[0]); no medial extrascapula is present in other species of *Phoxinus* (TS 67[1]).

Sphenotic (Fig.45A-D). The sphenotic is placed at the dorsolateral side of the neurocranium in cyprinids. Dorsally, the sphenotic sutures the frontal anteromesially, the parietal posteromedially, and the pterotic posteriorly. Ventrally, the sphenotic sutures the pterosphenoid anteriorly and the prootic posteriorly. The bone forms the hyomandibular fossa ventrolaterally.

In *Phoxinus* the sphenotic is irregularly shaped. Generally, its middle portion is broader than its anterior and posterior portion. Dorsally, the anterior portion of the lateral margin of the sphenotic is deeply concave in *P. cumberlandensis* and *neogaeus* (TS 68[1]); the anterior portion of the lateral margin of the bone is shallowly concave in other species of *Phoxinus* (TS 68[0]).

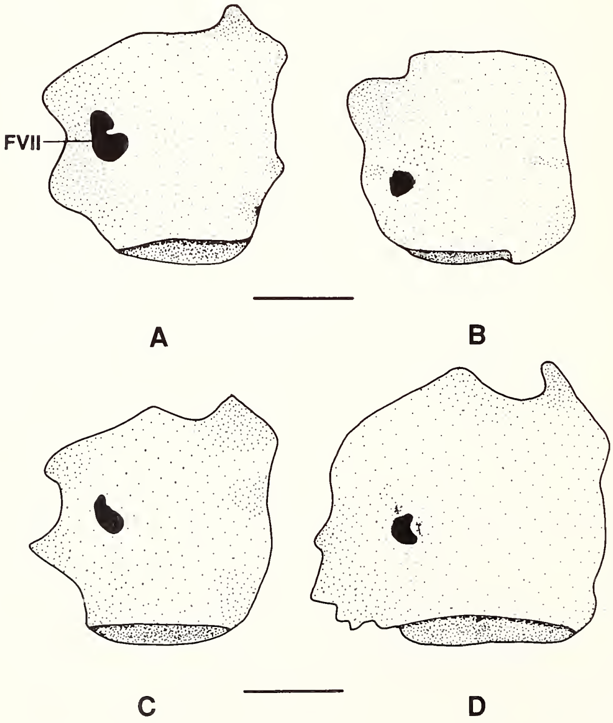

Fig.46: Lateral view of prootic of some species of *Phoxinus*. A: *P. oreas* (KU 3259, 55.0 mm SL); B: *P. eos* (KU 12255, 43.0 mm SL); C: *P. erythrogaster* (KU 5773, 51.5 mm SL); D: *P. neogaeus* (KU 8521, 53.0 mm SL). Scale bars = 1 mm.

Ventrally, the sphenotic bears three to five concavities which are separated from one another by bony ridges. In *P. phoxinus* and *cumberlandensis*, three concavities are present (TS 69[2]). In *P. eos* and *erythrogaster*, there are four concavities (TS 69[0]). Five concavities were found in other species of *Phoxinus* (TS 69[1]).

In the outgroups, the sphenotic is not deeply concave at the anterior portion of the lateral margin, and bears four concavities on its ventral side.

Prootic (Fig.46A-D). In cyprinids, the prootic is placed at the ventral side of the neurocranium. It sutures with sphenotic anterodorsally, pterotic and epioccipital posterodorsally, exoccipital and basioccipital posteriorly, parasphenoid ventrally, and pterosphenoid anteriorly.

In *Phoxinus* the prootic is an irregularly shaped plate-like bone forming a major portion of the posterolateral wall of the braincase. The prootic bears a notch at its anterior margin. This notch and the one at the posterior margin of the pterosphenoid form the trigeminal foramen. The notch on the anterior margin of the prootic is deeper in *P. erythrogaster* and *oreas* (TS 70[1]) than in other species of *Phoxinus* (TS 70[0]). The prootic also bears a facial foramen at its middle portion. A process is present on the dorsal margin of the prootic in some *Phoxinus* species. The process is well-developed in *P. neogaeus*, less developed in *P. oreas, erythrogaster*, and *cumberlandensis* (TS 71[0]), and it is absent in other species of the genus (TS 71[1]). Ventrally, the prootic is forked and articulates with the parasphenoid.

In the outgroups, the prootic bears a shallow notch at its anterior margin and a process at its dorsal margin.

Epioccipital (Fig.47A-C). This bone was first named as epiotic by Huxley (1858). Patterson (1975) showed that the bone is an ossification of the occipital arch invading into the otic region, thus he proposed "epioccipital" to replace "epiotic" for the bone. In cyprinids, the epioccipital is a paired endochondral bone, located at the posterior portion of the neurocranium. Dorsally, the epioccipital sutures the supraoccipital mesially, pterotic laterally, and parietal anteriorly. Ventrally, the epioccipital sutures the exoccipital and prootic mesially, the exoccipital and pterotic posteriorly, and pterotic laterally. Posteriorly, the epioccipital sutures the exoccipital ventrally, supraoccipital mesially, and the pterotic laterally.

In cyprinids, a subtemporal fossa is formed by the posterior side of the prootic as the inner wall of the fossa, the dorsoposterior portion of the pterotic, and epioccipital as roof of the fossa. In most cyprinids, including *Phoxinus* and the outgroups, the fossa is relatively deep and circular or oval in shape (Howes 1981).

In *Phoxinus*, the epioccipital is a complicated bone in morphology. Dorsally, the bone is plate-like with a process at its posterior edge. The general shape of the bone in a dorsal view varies among species. In *P. cumberlandensis*, the epioccipital is much narrower at its anterior portion than at its posterior portion and, therefore, is triangular-shaped (TS 72[1]). In other species of the genus, the bone is more or less rectangular (TS 72[0]). In *P. phoxinus, brachyurus*, and *issykkulensis*, the process on the posterior margin is large and blunt (TS 73[1]; Fig.47B). In other species of *Phoxinus*, the process is narrow and elongated (TS 73[0]), either sharp (e.g., *P. cumberlandensis*), or blunt (e.g., *P. neogaeus*).

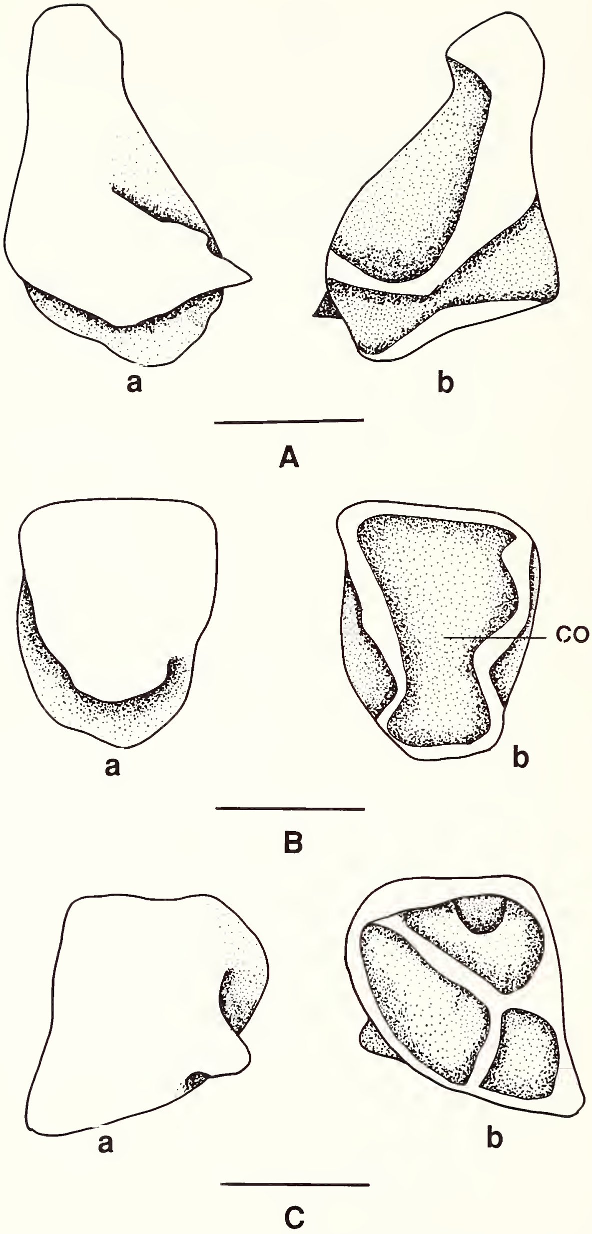

Fig.47: Epioccipital of *Phoxinus* (a: dorsal view; b: ventral view). A: *P. cumberlandensis* (KU 18934; 52.0 mm SL); B: *P. phoxinus* (CNUC uncat., 76.0 mm TL); C: *P. neogaeus* (KU 8521, 53 mm TL). Scale bars = 1 mm.

The epioccipital bears two or three concavities on its ventral aspect. The concavities are separated one another by ridge-like structures. In *P. neogaeus*, the anterior concavity bears another deeper "subconcavity" at its anterior portion (TS 74[1]; Fig.47C). The "subconcavity" is absent in other species of *Phoxinus* (TS 74[0]).

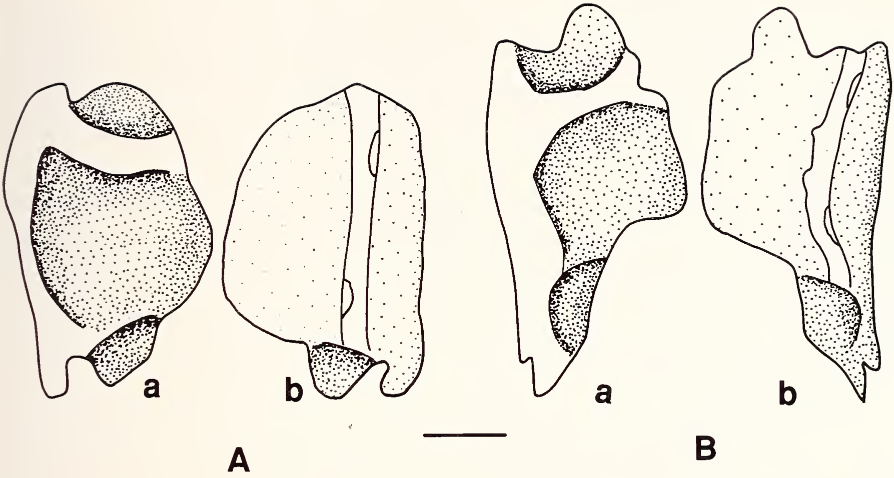

Fig.48: Pterotic of (A) *Phoxinus erythrogaster* (KU 5773, 51.5 mm SL), and (B) *P. cumberlandensis* (KU 18934, 52.0 mm SL) (a: ventral view; b: dorsal view). Scale bars = 1 mm.

In the outgroups, the epioccipital is more or less rectangular; it bears a small sharp process at its posterior margin, and its anterior concavity on the ventral side bears no small deeper "subconcavity".

Intercalar. The intercalar is a small paired endochondral bone placed at the posteroventral side of the pterotic. It is triangular in shape and does not vary significantly among *Phoxinus* species.

Pterotic and lateral extrascapula (Figs.44A, B; 48A, B). Dorsally, in *Phoxinus*, the pterotic sutures the sphenotic anteriorly and epioccipital posteromedially. Ventrally the pterotic sutures the sphenotic anteriorly, the prootic mesially, and the exoccipital posteriorly. The dorsal aspect of the pterotic is partially overlapped by the lateral extrascapular and the posttemporal in some species of the genus. The posterior portion of the pterotic forms the anterior part of the subtemporal fossa, and the lateral portion of the pterotic forms the dorsolateral portion of hyomandibular fossa.

The pterotic is irregular-shaped in *Phoxinus*. The dorsal aspect (dermopterotic) of the pterotic is plate-like. The otic canal of the cephalic lateral line runs on the dorsal side of the bone. At the anterior part of the bone, an anteriorly directed process is present in most *Phoxinus* species (TS 75[1]), but the process is absent in *P. tennesseensis, oreas*, and *erythrogaster* (TS 75[0]). A posteriorly directed process varying among the *Phoxinus* species exists on the posterolateral margin of the pterotic. The process is long and acute in *P. cumberlandensis* (TS 76[1]), but short and blunt in other species of *Phoxinus* and in the outgroups (TS 76[0]).

Ventrally, the pterotic bears two concavities, i.e., the anterior and posterior concavities separated by ridges. The anterior concavity, with the concavity formed by prootic, forms the otic capsule. The medial concavity forms part of subtemporal fossa.

A lateral extrascapular is present on the posterior portion of the pterotic in *P. brachyurus* (TS 77[1]). The lateral extrascapular is a small bar-shaped bone bearing a part of the supratemporal canal of the cephalic lateral line canal. No lateral extrascapular is present in other species of *Phoxinus* and in the outgroups (TS 77[0]).

Occipital Region

The occipital region is the most posterior region of the skull. It forms the posterodorsal cover and the posterior wall of the braincase. Bones in the region include exoccipital and supraoccipital. The former is paired, and the latter is single. The basioccipital will be described in the basicranial region.

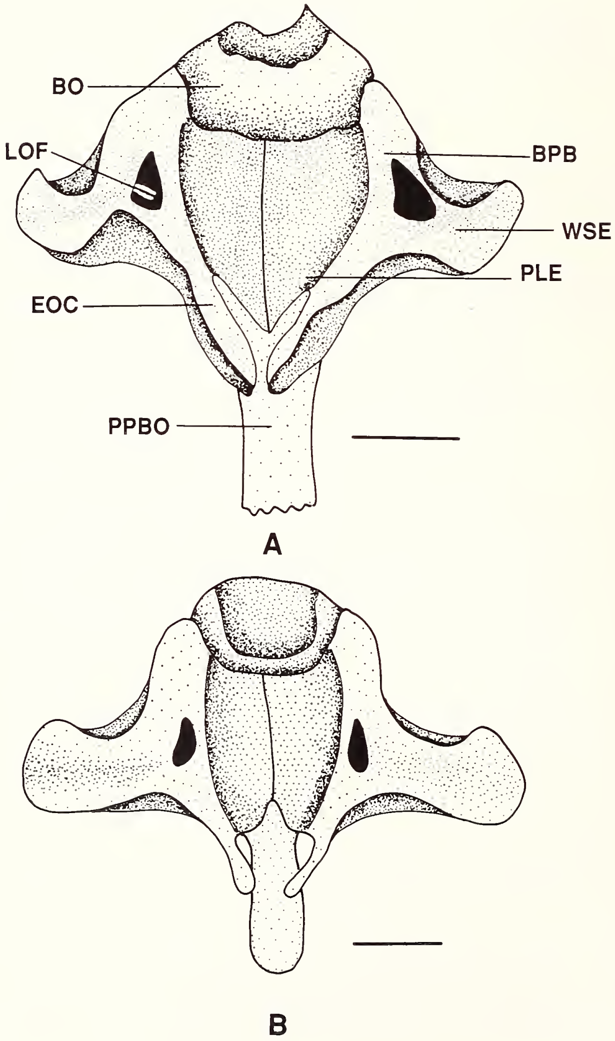

Fig.49: Dorsal view of posterior cranium (parietal removed) of (A) *Phoxinus phoxinus* (CNUC uncat., 76.0 mm TL), and (B) *P. cumberlandensis* (KU 18934, 52.0 mm SL). Scale bars = 1 mm.

Exoccipital (Figs.49A-B, 50). In cyprinids, the exoccipital is a paired endochondral bone placed at the posterior portion of the neurocranium. The exoccipital forms the ventral portion of the braincase's posterior wall and a part of the foramen magnum. The exoccipital sutures with the epioccipital and supraoccipital dorsally and basioccipital ventrally. On the ventral view, it sutures with the prootic anteriorly, basioccipital medially, epioccipital and pterotic anteriorly. The right and left exoccipitals suture one another mesially. A cavum sinus impar is present between the dorsal margin of the basioccipital and the middle portion of the ventral margin of the exoccipital.

Posteriorly, the exoccipital extends laterally and expands medially in *Phoxinus*. The mesial edge of the exoccipital is laterally concave, therefore the foramen magnum is formed between the two exoccipitals laterally and supraoccipital dorsally. A lateral occipital foramen is also formed on the exoccipital at the base near the medial margin. Viewed dorsally (after the supraoccipital and epioccipital removed), the left and right exoccipitals form a butterfly-shaped structure. Each of the two exoccipitals extends laterally to form the "wing" portion of the "butterfly" (Figs.49A-B, 50), and the middle part of the bone forms the "body" (Figs.49A-B, 50). At the median of the exoccipital is a thin and flat plate-like portion (Figs 49A-B, 50) which meets its counter part at the medial side of the exoccipital. The plate-like portion of the basioccipital bears two dorsal crests at the dorsal aspect of the bone (see also the description of basioccipital below). These two dorsal crests of the basioccipital form a canal whereas the plate-like structure of the exoccipital roofs the canal-like structure (Fig.50).

Variation of the exoccipital among the *Phoxinus* species includes shape of the wing portion and the posterior margin of the plate portion. In *P. phoxinus, neogaeus*, and *issykkulensis*, the anterior margin of the wing-like structure is deeply concave (TS 78[1]); the margin is shallowly concave in other species of *Phoxinus* (TS 78[0]). The posterior margin of the plate-like structure is convex in *P. neogaeus, issykkulensis*, and *phoxinus* (TS 79[1]); it is shallowly concave in *P. eos*, and *erythrogaster*, and deeply concave in other species of *Phoxinus* (TS 79[0]).

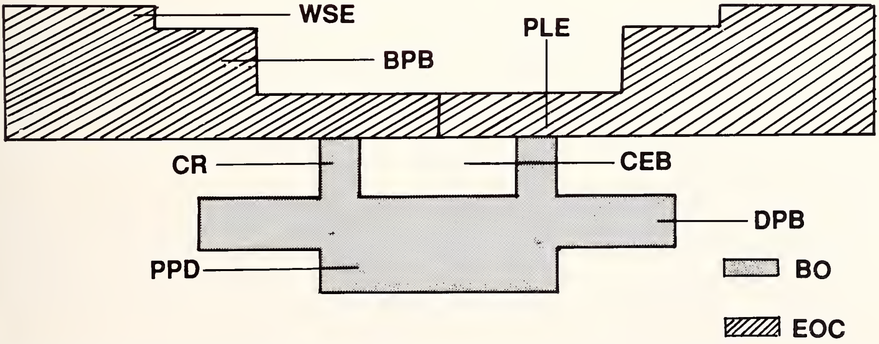

Fig.50: Diagram showing the relationships between basioccipital and exoccipitals (anterior view) of *Phoxinus*.

In the outgroups, the anterior margin of the wing-like structure is shallowly concave, and the posterior margin of the plate-like portion of the exoccipital is concave.

Supraoccipital and medial extrascapula (Figs.44A, B, 51A-C). In cyprinids, the supraoccipital is a medial bone and placed at the most posterior portion of the dorsal side of neurocranium and forms the posterior roof of the braincase. Size of the crest varies greatly in the cyprinids from well-developed (e.g., *Luciobrama macrocephalus, Ctenopharyngodon idellus* – Howes 1978, 1981) to poorly developed (e.g., *P. phoxinus*).

Dorsally, the supraoccipital is overlapped by the parietal anteriorly and contacts with the epioccipital laterally in *Phoxinus*. Posteriorly, the supraoccipital sutures with the epioccipital and the exoccipital laterally and exoccipital ventrally. The supraoccipital forms the middle portion of the posterior cover of the braincase and the dorsal edge of the foramen magnum.

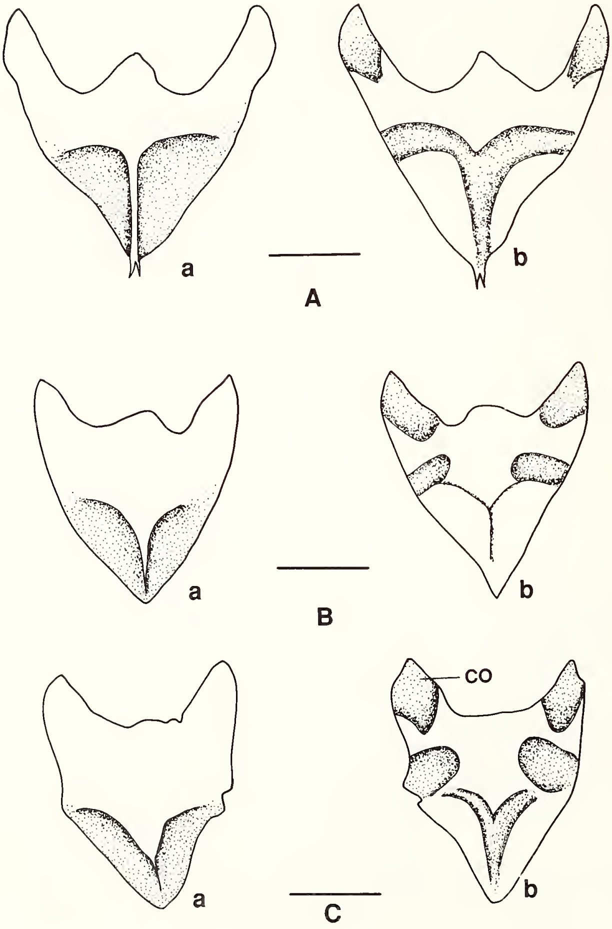

Fig.51: Supraoccipital of *Phoxinus* (a: dorsal view; b: ventral view). A: *P. phoxinus* (CNUC uncat., 76.0 mm TL); B: *P. erythrogaster* (KU 5773, 51.5 mm SL); C: *P. cumberlandensis* (KU 18934; 52.0 mm SL). Scale bars = 1 mm.

In *Phoxinus*, the dorsal portion of the supraoccipital is a flat plate, the posterior portion of the flat plate is bent ventroposteriorly. Viewed dorsally, the middle of the anterior margin of the supraoccipital is deeply concave. Therefore, two anterior processes are present at the lateral portion of the anterior margin of the bone. The crest at the posterior part of the flat plate extends posteriorly. The crest is poorly developed, and is attached by ligaments from the Weberian apparatus and the supraneural bones. Posteriorly, the bone is triangular in shape. The posterior surface of the supraoccipital is attatched by epaxial muscles. Four concavities are present on the ventral aspect of the bone (Fig.51A-C).

Variation of the supraoccipital within *Phoxinus* includes the anterior margin and the concavities at the ventral aspect of the bone. In *P. brachyurus, issykkulensis, phoxinus, erythrogaster, tennesseensis, oreas*, and *neogaeus*, a process is present at the middle of the anterior margin (between the two anterior processes at the anterior margin) (TS 80[1]). The process is well developed in all of the above species, except *P. erythrogaster* in which the process is very short. In *P. cumberlandensis* and *eos*, no process is present at the middle of the anterior margin between the two anterior processes (TS 80[0]). In *P. cumberlandensis*, the four concavities on the ventral side of the supraoccipital are more developed and deeper (TS 81[1]) than that in other species of *Phoxinus* (TS 81[0]).

A small bar-like medial extrascapular (Fig.44B) is present on the supraoccipital in *P. brachyurus* (TS 82[1]). This medial extrascapula is not present in other species of *Phoxinus* (TS 82[0]; Fig.45A).

In the outgroups, the middle of the anterior margin of the supraoccipital bears no process, the concavities on the ventral side of the supraoccipital are small and shallow; the medial extrascapula is absent on the supraoccipital.

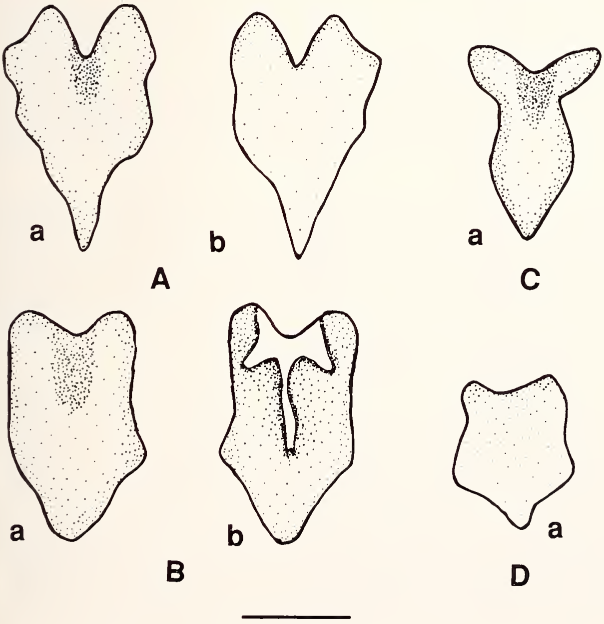

Fig.52: Vomer of *Phoxinus* (a: ventral view; b: dorsal view). A: *P. phoxinus* (CNUC uncat., 76.0 mm TL); B: *P. erythrogaster* (KU 5773; 51.5 mm SL); C: *P. oreas* (KU 3259, 55 mm SL, ventral view); D: *P. eos* (KU 12255, 43.0 mm SL, ventral view). Scale bars = 1 mm.

Basicranial Region

The basicranial region forms the base of the braincase. Three single bones – vomer, parasphenoid, and basioccipital – are included in this region.

Vomer (Fig.52A-D). In cyprinids, the vomer is a single bone, located at the most anteroventral portion of the neurocranium. Dorsally, the vomer connects with the mesethmoid via the planum ethmoidale, as discussed above. Anteriorly, it attaches the kinethmoid via ligaments. The anterolateral edge sutures with the preethmoid.

In *Phoxinus*, the vomer is a plate-like bone bearing a notch at its anterior margin, a constriction at its lateral margin to form a waist, and a process at its posterior margin extending posteriorly and overlapping the ventral side of the parasphenoid.

The process of the posterior margin of the vomer is elongated and sharp in *P. phoxinus* (TS 83[1]); this process is short and blunt in other species of *Phoxinus* and in the outgroups (TS 83[0]). A T-shaped ridge is present at the anterior part of the vomer's dorsal side in *P. erythrogaster* (TS 83[1]); the ridge is not observed in other species of *Phoxinus* and in the outgroups (TS 84[0]).

Parasphenoid (Fig.53A-G). The parasphenoid in cyprinids is a dermal bone and can only be observed in a ventral view of the neurocranium. It is underlaid anteriorly by the vomer.

In cyprinids, the parasphenoid sutures with the lateral ethmoid, orbitosphenoid, pterosphenoid, and prootic dorsally from anterior to posterior. The orbitosphenoid connects with parasphenoid via the orbital septum, as discussed above (however, in some minnows, e.g., *Crossocheilus, Labeo, Barbus*, the parasphenoid bears a dorsal ridge, via which the parasphenoid contacts with the orbital septum – Ramaswami 1955a, Chen et al. 1984); the pterosphenoid has only a small portion suturing with the ascending wing of the parasphenoid (see below). The posterior part of the parasphenoid overlaps the ventral side of the basioccipital ventrally. The anterior portion of the parasphenoid (anterior to the ascending wing) is generally narrower than the posterior portion (posterior to the ascending wing) in cyprinids.

In *Phoxinus*, the parasphenoid is an elongated plate-like bone; a laterodorsally extending ascending wing is present at the middle of the parasphenoid; the anterior portion of the bone is much narrower than the posterior portion. The anterior portion decreases in size posteriorly. Dorsally, a ridge at the middle of the anterior portion is present which contacts with the orbital septum. The ridge is well-developed in *P. phoxinus* and *eos* (TS 85[1]), and less developed in other *Phoxinus* species (TS 85[0]).

The ascending wing is more or less triangular and bent dorsally. A notch is present on the posterior edge of each ascending wing and, with the prootic, forms the carotid foramen. The notch is well-developed in *P. neogaeus, oreas, issykkulensis, brachyurus*, and *phoxinus* (TS 86[0]); it is less developed in other species of *Phoxinus* (TS 86[1]).

The posterior end of the parasphenoid is forked (Fig.53A-G). The fork is deep and extends to the middle of the posterior part of the parasphenoid in *P. phoxinus* (TS 87[1]); the fork is much shallower in *P. brachyurus, erythrogaster, eos, oreas, neogaeus, tennes-*

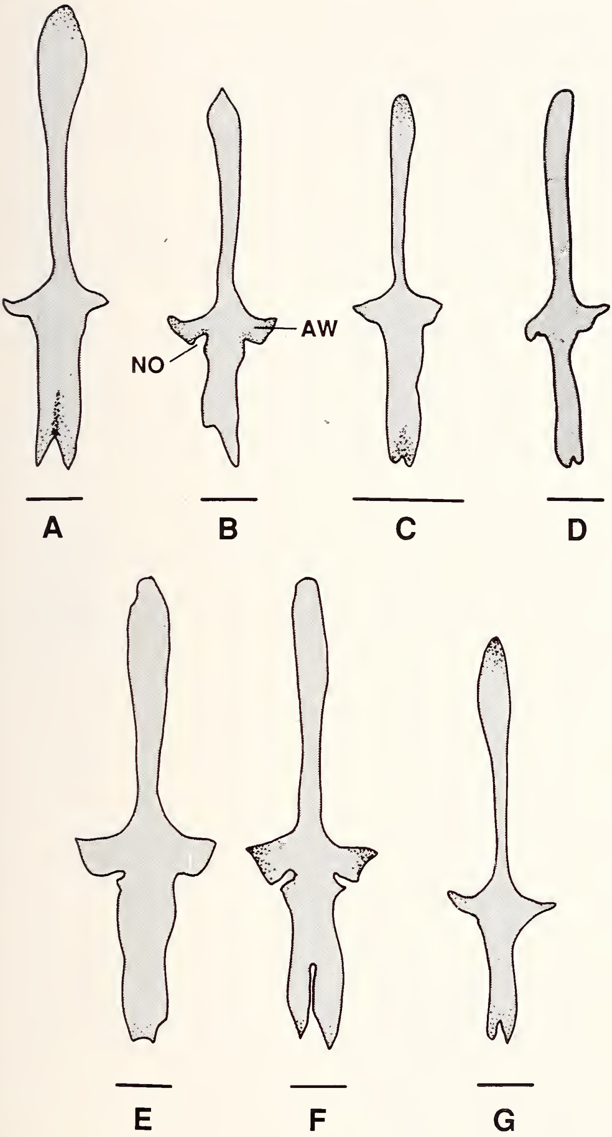

Fig.53: Parasphenoid in ventral view of *Phoxinus*. A: *P. tennesseensis* (UT 44.5274, 50.0 mm SL); B: *P. oreas* (KU 3259, 55.0 mm SL); C: *P. eos* (KU 12255, 43.0 mm SL); D: *P. cumberlandensis* (KU 18934, 52.0 mm SL); E: *P. neogaeus* (KU 8521, 53.0 mm SL); F: *P. phoxinus* (CNUC uncat., 76.0 mm TL); G: *P. erythrogaster* (KU 5773, 51.5 mm SL). Scale bars = 1 mm.

seensis, issykkulensis, and *cumberlandensis* (TS 87 [0]); the fork is almost absent in *P. neogaeus*.

The posterior portion of the parasphenoid overlaps the ventral side of the basioccipital. The extent of the overlap varies among species of *Phoxinus*. The posterior end of the parasphenoid extends to the middle of the dorsal part of the basioccipital in *P. neogaeus,* *brachyurus, issykkulensis*, and *phoxinus* (TS 88 [1]); the posterior end of the bone extends to the posterior portion of the dorsal part of the basioccipital in other *Phoxinus* (TS 88[0]).

In the outgroups, the parasphenoid bears a poorly-developed dorsal ridge on its dorsal side, and a well-developed notch on the posterior margin of the ascending wing; the posterior end of the bone is shallowly forked and extends to the posterior portion of the ventral aspect of the basioccipital's dorsal part.

Basioccipital (Figs.49A-B, 50, 54A-B, 55A-D). In cyprinids, the basioccipital is placed at the most posteroventral portion of the neurocranium, and forms the posterior base of the braincase. It sutures with exoccipital dorsally and laterally, prootic anteriorly, and parasphenoid anteroventrally.

The basioccipital is morphologically a complex bone in cyprinids. (It might be the most complicated in all the bones in cyprinids.) Basically, two parts can be recognized from the bone – i.e., dorsal portion, and a pharyngeal process. The dorsal portion appears as a flat plate and is the anterodorsal portion of the basioccipital. The pharyngeal process is the portion located at the posteroventral side of the dorsal portion of the basioccipital (Figs.54A-B, 55A-D). The pharyngeal process consists of a bony plate (pharyngeal pad) for the attachment of a horny pad, a process located at the posterior margin of the pharyngeal pad (posterior process) (Ramaswami 1955a), and an anterior process (in some species). The posterior side of the pharyngeal pad forms the concave condyle articulating with the anterior side of vertebra 1. The dorsal aorta passes the fenestra formed between

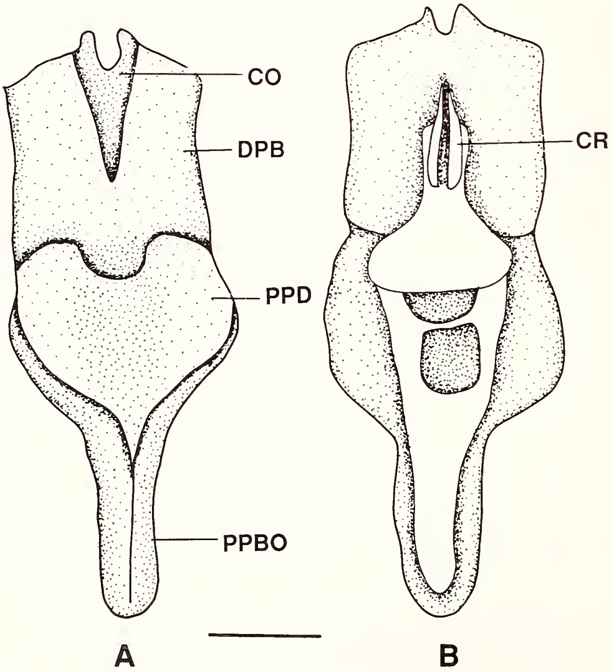

Fig.54: Basioccipital bone of *Phoxinus neogaeus* (KU 8521, 53.0 mm SL) (A: ventral view; B: dorsal view). Scale bar = 1 mm.

the ventral side of the dorsal portion and the dorsal side of the pharyngeal process. The posterior process was formed by the haemal arches of the third vertebral segment assimilated into the skull; the centrum of the vertebral segment was united by the basioccipital to form the condyle (Ramaswami 1955a).

The basic morphology of the basioccipital in *Phoxinus* is similar to that in other cyprinids described above. Variations among the species of *Phoxinus* include the following aspects.

In *P. oreas, neogaeus*, and *phoxinus*, a notch is present on the middle of the anterior margin of the basioccipital (TS 89[1]); the notch is absent on the anterior margin in other species of *Phoxinus* (TS 89[0]). In all *Phoxinus* species, a shallow and elongated concavity is present at the anteromiddle portion of the ventral side of the dorsal portion (of the basioccipital) on which the parasphenoid overlaps. In *P. neogaeus, phoxinus, brachyurus*, and *issykkulensis*, the concavity is triangular and extends to the anterior half of the dorsal portion (TS 90[1]). In other species of *Phoxinus*, however, the concavity is rectangular and extends to the posterior half of the dorsal portion of the basioccipital (TS 90[0]).

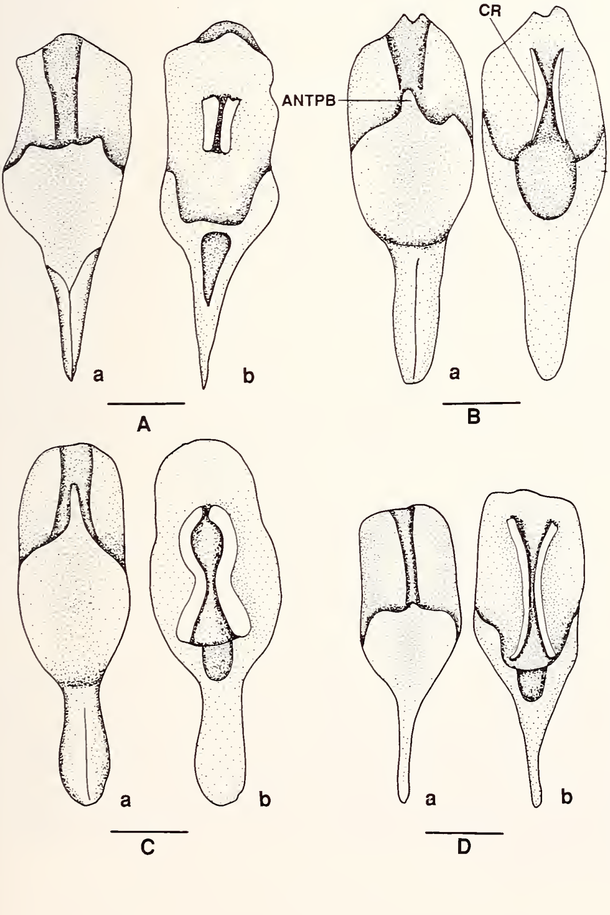

Fig.55: Basioccipital of *Phoxinus* (a: ventral view; b: dorsal view). A: *P. erythrogaster* (KU 5773, 51.5 mm SL); B: *P. oreas* (KU 3259, 55.0 mm SL); C: *P. cumberlandensis* (KU 18934, 52.0 mm SL); D: *P. eos* (KU 12255, 43.0 mm SL). Scale bars = 1 mm.

Dorsally, two anteroposteriorly directed parallel crests (Figs.54B, 55A-D) are present on the mesial portion of the dorsal side of the basioccipital's dorsal portion. These two parallel crests articulate with the ventral side of the exoccipital to form a canal-like structure (see the description of the exoccipital above) (Figs.49A-B, 50). The crests run from the middle to the posterior end of the dorsal portion of the basioccipital. Variation of the crest includes the space between the anterior ends of the left and right crests, and the extent of the development of the crest. The crest is high and the space between the anterior ends of the left and right crests is narrow in *P. cumberlandensis* (TS 91[1]; Fig.55C); whereas the crest is lower and the space is broad in other *Phoxinus* species (TS 91[0]). In *P. erythrogaster*, the crest is short, and placed at the middle of the dorsal side of the dorsal portion (TS 92[1]; Fig.55A). In other *Phoxinus*, the crest is elongated extending from the middle to the posterior margin of the dorsal side of the dorsal portion (TS 92[0]; Fig.55B-D).

As described above, three parts can be recognized for the pharyngeal process in most species of *Phoxinus*, i.e., the pharyngeal pad, the anterior process (lacking in some species, see below) located at the anterior margin of the pharyngeal pad, and the posterior process. The pharyngeal pad is a plate-like structure contacting the masticatory pad at its ventral side. The pharyngeal pad is concave; its margin extends anteriorly forming the anterior process in some species, its posterior margin extends forming the posterior process. Variations were observed in size and shape of the pharyngeal pad, the anterior process, and the posterior process. The pharyngeal pad is well developed, semi-ellipsoidal, elongated and relatively narrow, the length between the anterior and posterior margins (the anterior and posterior processes not included) is longer than the width between the left and right margins of the pad, the ventral concavity is deep in *P. tennesseensis, oreas*, and *cumberlandensis* (TS 93[1]). In other *Phoxinus* species, the pharyngeal pad is less developed, semi-round, short and relatively wide, its length is shorter than its width, and the concavity is shallow (TS 93[0]).

The anterior process is long and narrow in *P. cumberlandensis* (Fig.55C), whereas the anterior process is short and broad in *P. oreas, tennesseensis, issykkulensis*, and *phoxinus*; it is less developed in *P. eos* (Fig.54D) and very small, almost absent in *P. erythrogaster* (TS 94[0]; Fig.55A). In *P. brachyurus* and *neogaeus*, the anterior process is absent, and the anterior margin of the pharyngeal pad is concave (TS 94[1]). Besides the main anterior process mentioned above, two small anterior processes are present at the lateral part of the anterior margin of the pharyngeal pad in *P. phoxinus* (TS 95[1]) (Fig.13C). The lateral processes are absent in other species of *Phoxinus* (TS 95[0]). The posterior process is broader and stout in *P. neogaeus, oreas, cumberlandensis*, and *tennesseensis* (TS 96 [1]). This process is relatively high and narrow in other *Phoxinus* (TS 96[0]).

In the outgroups, the anterior margin of the dorsal portion is straight or slightly convex without concavity; the concavity at the ventral side of the dorsal portion is elongated and rectangular; the crest on the dorsal side of the dorsal portion of the basioccipital is straight, and the space between the anterior ends of the crests is wide; the pharyngeal pad is relatively small and short; the anterior process is not present on the anterior margin of the pharyngeal margin (no lateral process present at the lateral portion of the anterior margin), and the posterior process is narrow.

Presence of the anterior process of the pharyngeal process is previously proposed as an apomorphic character at the genus level for *Phoxinus* (see p. 34). Absence of the process in *Phoxinus* may have resulted from loss or is a reversal of the presence of the process. Therefore, the absence of the process is hypothesized an apomorphic character state within *Phoxinus*.

Viscerocranium

The viscerocranium is located ventrally to the neurocranium. The regions included in the viscerocranium are the upper and lower jaws, hyoid region, suspensorium, opercular region, and branchial region.

Upper jaw

As in all cyprinids, the upper jaw in *Phoxinus* consists of two paired bones: premaxilla and maxilla.

Premaxilla (Fig.56A-E). The premaxilla is an elongated, narrow plate-like bone bearing an ascending process at its anterior portion which contacts with the same process of other premaxilla. The premaxilla tapers posteriorly; therefore, its posterior portion is narrower than its anterior portion. The morphology of the premaxilla varies inter- and intraspecifically.

Maxilla (Figs.57A-C, 58A-E). In cyprinids, the maxilla is a paired elongated plate-like bone. Five processes can be recognized from the maxilla (Ramaswami 1955a). Following Chen (1986b), these five processes were named as the anterior process, anterior ascending process, anteromedial process, posterior ascending process, and posterior process (Fig.57C). These processes show variations among the *Phoxinus* species.

The anterior process (Fig.57C) is the most anterior portion of the maxilla. It is broad and blunt in *P. erythrogaster, issykkulensis, phoxinus, oreas*, and *neogaeus* (TS 97[1]); it is narrow and sharp in *P. brachyurus, cumberlandensis, tennesseensis*, and in the outgroups (TS 97 [0]).

The anteromedial process is the process located at the medial side of the anterior process (Figs.57A-C, 58A-E). The anteromedial process is broad, blunt, and well developed in *P.*

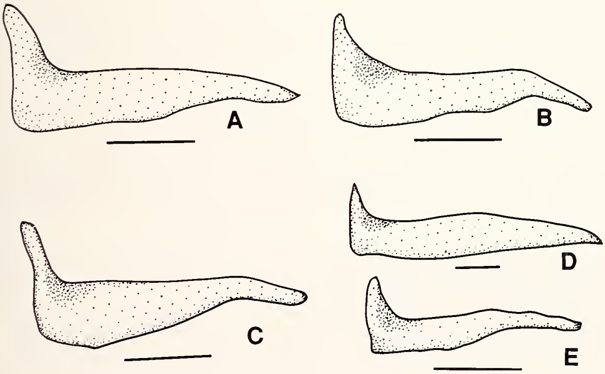

Fig.56: Premaxilla in lateral view of *Phoxinus*. A: *P. phoxinus* (CNUC uncat., 76.0 mm TL); B: *P. cumberlandensis* (KU 18934, 51.5 mm SL); C: *P. oreas* (KU 3259, 55.0 mm SL); D: *P. erythrogaster* (KU 5773, 51.5 mm SL); E: *P. eos* (KU 12255, 43.0 mm SL). Scale bars = 1 mm.

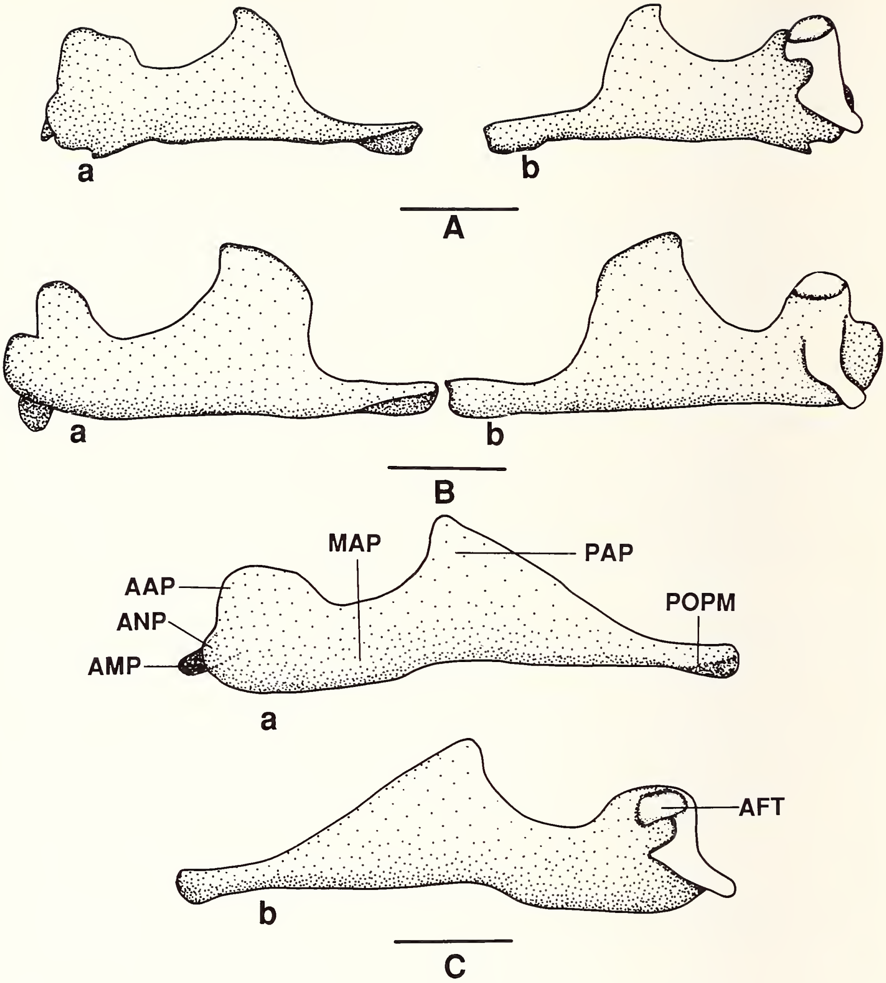

Fig.57: Maxilla of *Phoxinus* (a: lateral view; b: medial view). A: *P. oreas* (KU 3259, 55.0 mm SL); B: *P. phoxinus* (CNUC uncat., 76.0 mm TL); C: *P. neogaeus* (KU 8521, 53.0 mm SL). Scale bars = 1 mm.

oreas, neogaeus, cumberlandensis, brachyurus, tennesseensis, erythrogaster, and *phoxinus* (TS 98[1]); it is sharp and less developed in *P. eos* (TS 98[0]); it is almost absent in *P. issykkulensis* (TS 98[2]).

In the outgroups, the anteromedial process is sharp. The presence of the blunt process and the very small process are proposed herein to be derived independently.

The anterior ascending process (Fig.57C) was found on the dorsal side of the anteromedial process and extends dorsally. The process is lower, almost absent in *P. erythrogaster*

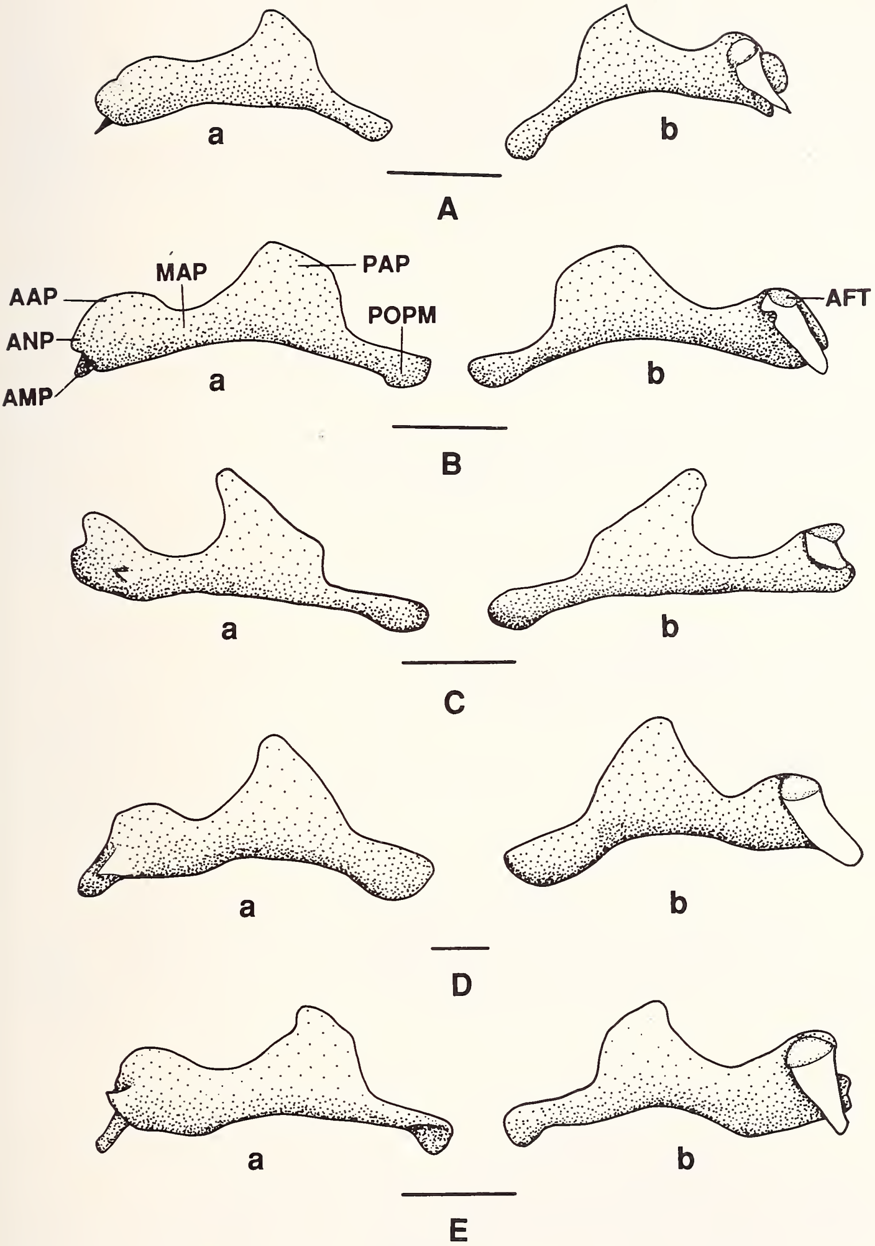

Fig.58: Maxilla of *Phoxinus* (a: lateral view; b; medial view). A: *P. eos* (KU 12255, 43.0 mm SL); B: *P. erythrogaster* (KU 5773, 52.5 mm SL); C: *P. issykkulensis* (P-10696; 42.4 mm SL); D: *P. brachyurus* (MCZ 3006, 75.9 mm SL); E: *P. cumberlandensis* (KU 18934, 52.0 mm SL). Scale bars = 1 mm.

and *P. eos* (TS 99 [1]); whereas it is high in other species of *Phoxinus* and in the outgroups (TS 99 [0]).

Viewed medially, an articulatory facet is present (Fig.57C). The facet is formed by both the dorsal side of the anteromedial process and the base of the anterior ascending process in *P. oreas, cumberlandensis, erythrogaster, tennesseensis, brachyurus, neogaeus*, and *eos* (TS 100 [1]); whereas the facet is formed only by the anterior ascending process in *P. phoxinus, issykkulensis*, and in the outgroups (TS 100[0]).

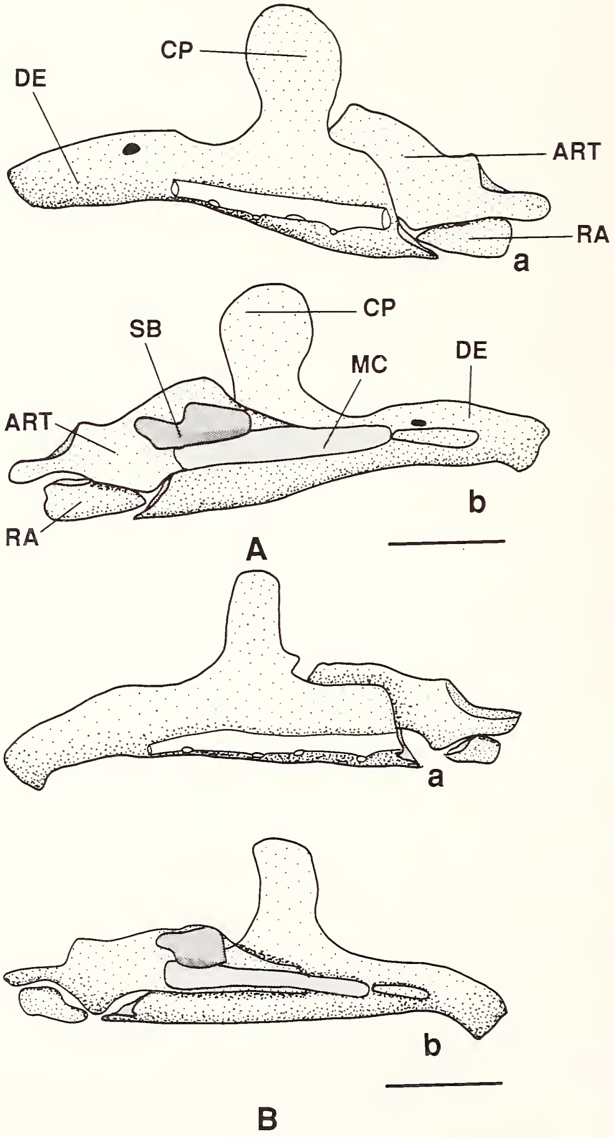

Fig.59: Lower jaw of *Phoxinus* in lateral (a) and medial (b) views. A: *P. phoxinus* (CNUC uncat.; 76 mm TL); B: *P. oreas* (KU 3259; 55.0 mm SL). Scale bars = 1 mm.

Extending dorsally, the posterior ascending process is located at the posterior portion of the maxilla. It is high and relatively narrow in *P. oreas* and *issykkulensis* (TS101 [1]); it is broad in other species of *Phoxinus* and in the outgroups (TS 101[0]).

The posterior process is the most posterior portion of the maxilla. It extends ventroposteriorly in *P. brachyurus, cumberlandensis, erythrogaster, issykkulenis, eos*, and in the outgroups (TS 102[0]); it extends posteriorly in other species of *Phoxinus* (TS 102[1]).

Lower jaw

In cyprinids, the lower jaw is composed of five paired bones and cartilages, i.e., dentary, retroarticular, sesamoid bone, anguloarticular, and Meckel's cartilage. Ramaswami (1955a) did not mention the Meckel's cartilage in the lower jaw of cyprinids, whereas Sarbahi (1932) only described three bones, i.e., dentary, angular (= retroarticular), and articular (= anguloarticular) in *Labeo rohita*.

Dentary (Figs.59A-B, 60A-C, 61A-B). In *Phoxinus*, the dentary is the largest element of the lower jaw; it is L-shaped with a coronoid process at the posterodorsal portion of the bone. Its ventrolateral portion bears the mandibular canal. The anguloarticular, sesamoid bone, and Meckel's cartilage are attached to the medial side of the dentary and the retroarticular to the ventroposterior portion of the dentary.

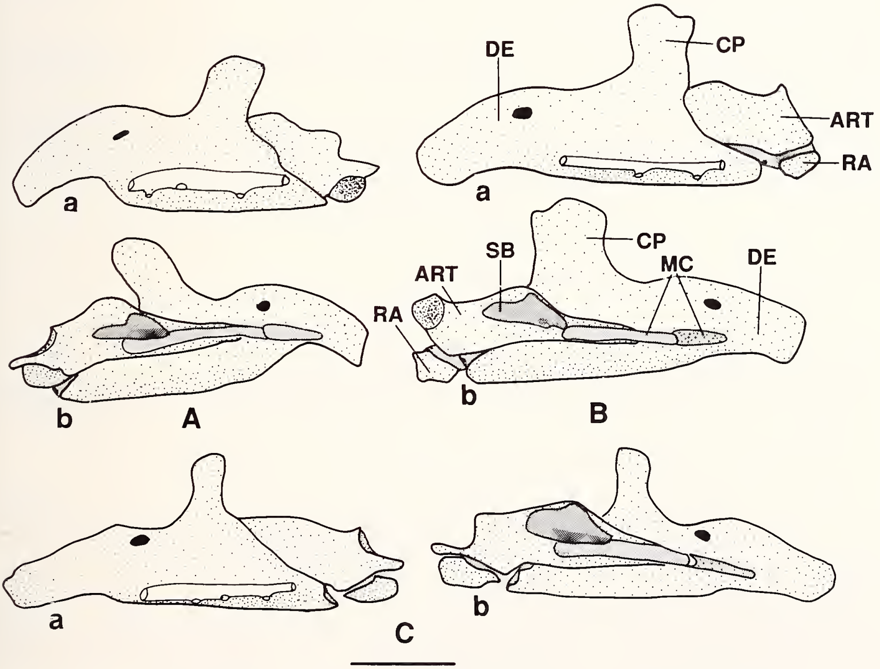

Fig.60: Lower jaw of *Phoxinus* in lateral (a) and medial (b) views. A: *P. eos* (KU 12255, 43.0 mm SL); B: *P. issykkulensis* (P-10696, 42.4 mm SL); C: *P. cumberlandensis* (KU 18934, 52.0 mm SL). Scale bars = 1 mm.

As a whole, the dentary is relatively short and blunt in *P. issykkulensis, brachyurus*, and *eos* (TS 103 [1]); it is relatively slender and elongated in other species of *Phoxinus* (TS 103[0]). The coronoid process is perpendicular to the anterior portion of the dentary, and not posteriorly sloped to the dorsal margin of the dentary in *P. cumberlandensis, issykkulensis, oreas*, and *phoxinus* (TS 104[1]); it is sloped to the dorsal margin of the dentary in other species of the genus (TS 104 [0]). The dentary is slender, and the coronoid process is sloped to the dorsal margin of the dentary in the outgroups.

Retroarticular (Figs.59A-B, 60A-C, 61A-B). The retroarticular is a triangular endochondral bone. It articulates with posteroventral side of the anguloarticular dorsally and ventroposterior portion of the dentary anteriorly. It is well-developed, its length is longer than one-third of the anguloarticular's total length in *P. phoxinus* (TS 105[1]). It is less developed, its length is much less than one-third of the anguloarticular's length in other species of *Phoxinus* and in the outgroups (TS 105[0]).

Sesamoid bone (or sesamoid articular) (Figs.59A-B, 60A-C, 61A-B). The sesamoid bone is a dermal element and located at the medial side of the anguloarticular and of the dentary. It is irregular-shaped with individual variations. The variation of phylogenetic significance is in the relationship between the sesamoid bone and the dentary. In *P. oreas, erythrogaster*, and *cumberlandensis*, about one-third of the sesamoid bone overlaps the dentary (TS 106[0]); whereas about half of the sesamoid bone overlaps the dentary in other species of *Phoxinus* (TS 106[1]).

In the outgroups, the sesamoid bone is knife-shaped and only one third of the bone overlaps the dentary.

Anguloarticular (Figs.59A, B, 60A-C, 61A-B). The anguloarticular is placed at posteromedial side of the dentary, and extends to middle of the dentary. The anguloarticular articulates with the retroarticular ventrally and with quadrate ventroposteriorly.

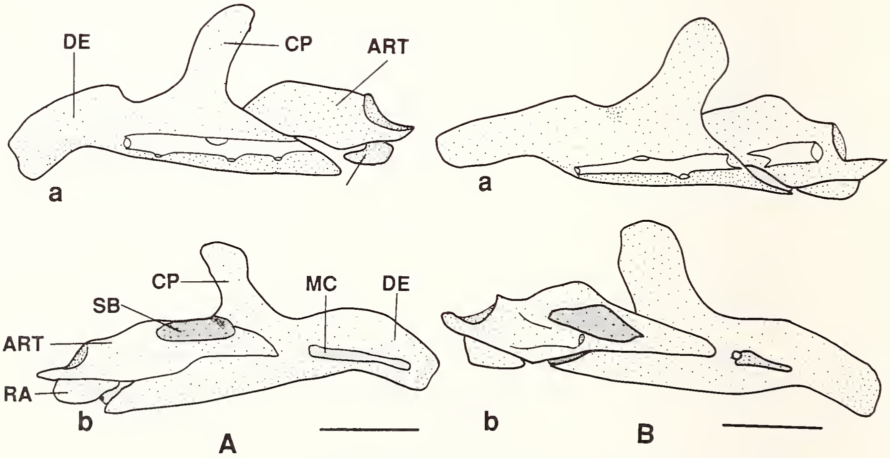

Fig.61: Lower jaw of some species of *Phoxinus* in lateral (a) and medial (b) views. A: *P. tennesseensis* (UT 44.5274, SL 50.0 mm); B: *P. erythrogaster* (KU 5773, SL 52.5 mm SL). Scale bars = 1 mm.

In *Phoxinus*, the anguloarticular is an irregular plate-like bone bearing an articular concavity at its posteroventral portion, a posterior process at the posterior margin, and an anterior process at the anterior margin. The posterior process and the articular concavity of the anguloarticular articulate with the quadrate. The posterior process of the anguloarticular is well-developed and elongated in *P. erythrogaster, tennesseensis, oreas, eos, cumberlandensis, phoxinus*, and in the outgroups (TS 107[0]); the process is less developed and short in other species of *Phoxinus* (TS 107[1]).

Meckel‘s Cartilage (Figs.59A, B, 60A-C, 61A-B). In cyprinids, the Meckel's cartilage is a bar-shaped and partially ossified cartilage in adults; it is placed at the medial side of the middle of the dentary, and the medial anterior portion of anguloarticular. The anterior portion of the cartilage ossifies during ontogeny. This ossified portion, called mentomecklian, is continuous to the unossified cartilaginous portion and can not be separated from the latter in *Phoxinus*. The shape of the Meckel's cartilage does not vary significantly among *Phoxinus* species. However, the cartilaginous portion is reduced into a very small part in *P. brachyurus* and *erythrogaster* (TS 108[1]); whereas it is not reduced in other species of *Phoxinus* and in the outgroups (TS 108[0]).

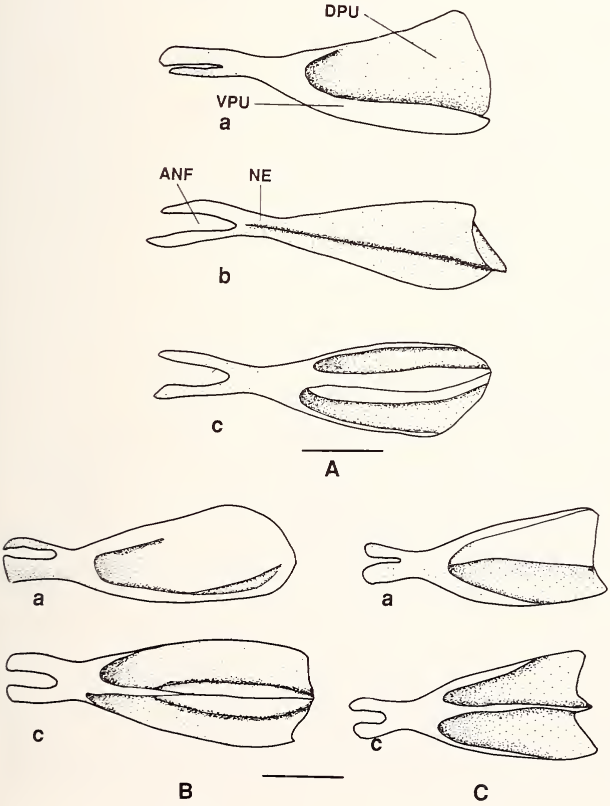

Fig.62: Urohyal of *Phoxinus* (a, lateral, b, ventral and c, dorsal views). A: *P. neogaeus* (KU 8521, 53.0 mm SL); B: *P. brachyurus* (MCZ 3006, 75.9 mm SL); C: *P. tennesseensis* (UT 44.5274, 50.0 mm SL). Scale bars = 1 mm.

Hyoid Region

This region is located posterior to the lower jaw and anterior to the ventral side of the hyomandibular. Via the symplectic and the hyomandibula, this region attaches to the neurocranium. Bones included in the region are the interhyal, posterior ceratohyal, anterior ceratohyal, hypohyal, basihyal, urohyal, and branchiostegals. Among them, the urohyal is formed as an "unpaired ossification of the tendon of the sternohyoideus muscle" (Arratia & Schultze 1990: 247), the branchiostegal rays are dermal elements, and the other are of chondral origin.

Urohyal (Figs.62A-C, 63A-D). In cyprinids, the urohyal is a single bone and placed medially along the ventral portion of the viscerocranium. The urohyal connects to the ventral hypohyal via ligaments anteriorly. The posterior part of the urohyal is attached by the large sternohyoid muscles to the pectoral girdle.

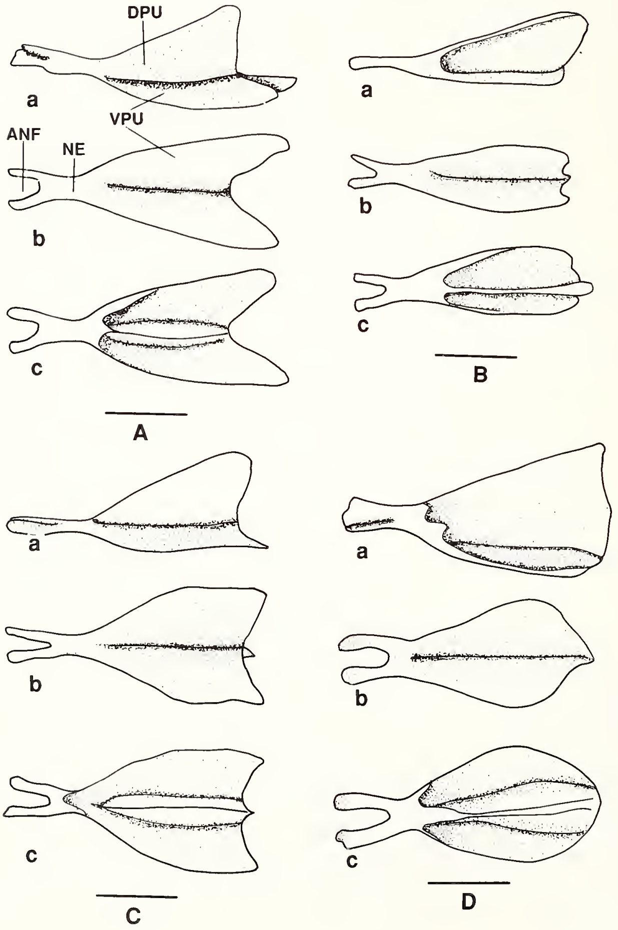

Fig.63: Urohyal of *Phoxinus* (a, lateral, b, ventral and c, dorsal views). A: *P. cumberlandensis* (KU 18934, 52.0 mm SL); B: *P. eos* (KU 12255, 43.0 mm SL); C: *P. erythrogaster* (KU 5773, 51.5 mm SL); D: *P. phoxinus* (CUNC uncat., 76.0 mm TL). Scale bars = 1 mm.

Several parts can be recognized in the urohyal, i.e., the ventral plate (= ventral spread of Kusaka 1974), dorsal plate (= dorsal spread of Kusaka 1974), anterior fork, and neck (Fig.63A). The thin ventral plate of the urohyal is located at the ventral portion of the bone. The bar-shaped neck is at the anterior to the ventral plate. The neck's anterior end is forked, forming the anterior fork of the urohyal. The anterior portion of the dorsal side of the ventral plate bears a concavity. Dorsally, the dorsal plate is present which extends

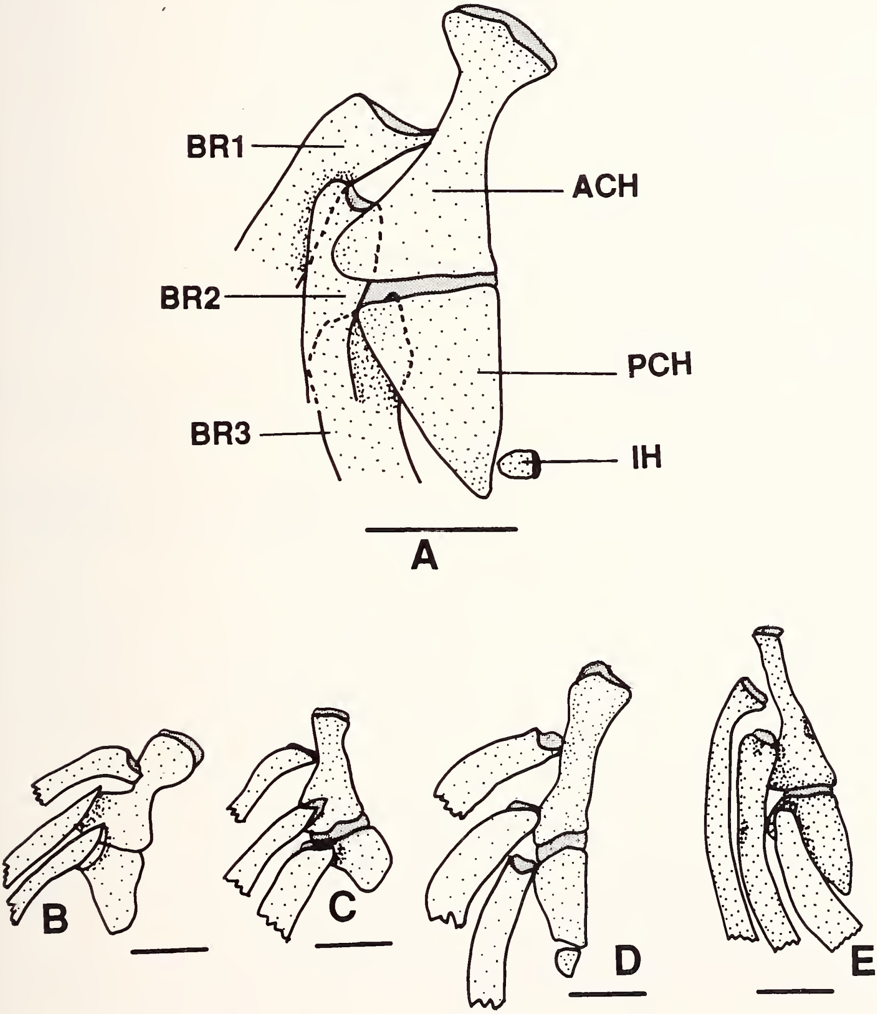

Fig.64: Lateral view of anterior and posterior ceratohyals, branchiostegals, and interhyal of *Phoxinus*. A: *P. oreas* (KU 3259, 55.0 mm SL); B: *P. phoxinus* (KU 22858, 58.0 mm SL); C: *P. eos* (KU 12255, 43.0 mm SL); D: *P. issykkulensis* (P-10696, 42.4 mm SL); E: *P. cumberlandensis* (KU 18934, 45.0 mm SL). Scale bars = 1 mm.

from the mesial line of the dorsal side of the ventral plate. The variations of the urohyal among *Phoxinus* species include the anterior fork, and the ventral and dorsal plates.

The anterior fork is deep in *Phoxinus neogaeus*, *phoxinus*, and *brachyurus* (TS 109[1]), its depth is more than two times of the neck length (from the most posterior point of the anterior fork to the anterior end of the ventral plate). The anterior fork is shallow and equals to (or less than) the neck length in other species of the *Phoxinus* (TS 109[0]).

The ventral plate is the main part of the urohyal. Generally, its posterior portion is broader than its anterior one. In *P. brachyurus*, *neogaeus*, and *phoxinus*, its posterior margin is convex (TS 110[1]). In other species of the *Phoxinus*, however, the posterior margin is concave (TS 110[0]). In *P. eos*, the concave posterior margin bears a process at middle.

The dorsal plate is perpendicular to the dorsal side of the ventral plate. It gradually increases in height posteriorly. Therefore, its posterior portion is higher than its anterior portion and the dorsal plate tends to be triangular in shape. In *P. cumberlandensis, oreas, erythrogaster*, and *tennesseensis*, the dorsal plate is high and short, its posterior margin is at the level of the most anterior point of the concave posterior margin of the ventral plate (TS 111[1]); in *P. brachyurus, issykkulensis, phoxinus*, and *neogaeus*, the dorsal plate is lower, its posterior margin is at the level of the most posterior point of the convexed posterior margin (TS 111[0]); in *P. eos*, the dorsal plate is lower and long, its posterior margin extends posterior to the posterior margin of the ventral plate.

In the outgroups, the depth of the anterior fork is less than the elongated neck length, the posterior margin of the ventral plate is shallowly concave; the dorsal plate is low and long, its posterior margin extends beyond the posterior margin of the ventral spread.

Branchiostegals (Fig.64A-E). In cyprinids, the branchiostegals include three pairs of thin, elongated plate-like slender dermal bones, branchiostegals 1, 2, and 3 (from the anterior to the posterior), and are placed at the ventrolateral side of the head.

Branchiostegal 1 (Fig.64A-E) is an elongated bone articulating with the anterior ceratohyal. The anterior end of branchiostegal 1 is concave in *P. neogaeus, issykkulensis, phoxinus, oreas, tennesseensis*, and *cumberlandensis* (TS 112[1]); the anterior end is convex in *P. erythrogaster, eos, brachyurus*, and in the outgroups (TS 112[0]). The relative position of the bone to the anterior ceratohyal does not vary significantly among the *Phoxinus* species.

Branchiostegal 2 (Fig.64A-E) articulates with posterior end of the anterior ceratohyal. The relative position between these two bones does not vary significantly among *Phoxinus* species. The anterior end of the branchiostegal is sharp in *P. phoxinus, erythrogaster, brachyurus*, and *eos* (TS 113[0]) which is similar to that in the outgroups. The anterior end of the branchiostegal 2 is blunt in other species of *Phoxinus* (TS 113[1]).

Branchiostegal 3 (Fig.64A-E) is the most posterior element of the branchiostegal rays. The position where the branchiostegal contacts the ceratohyals varies among species of *Phoxinus*. In *P. issykkulensis, phoxinus, erythrogaster, neogaeus*, and *brachyurus*, the anterior end of the branchiostegal 3 articulates with both the anterior portion of the posterior ceratohyal and the posterior portion of the anterior ceratohyal (TS 114[1]); branchiostegal 3 articulates with the anterior end of posterior ceratohyal only in other spe-

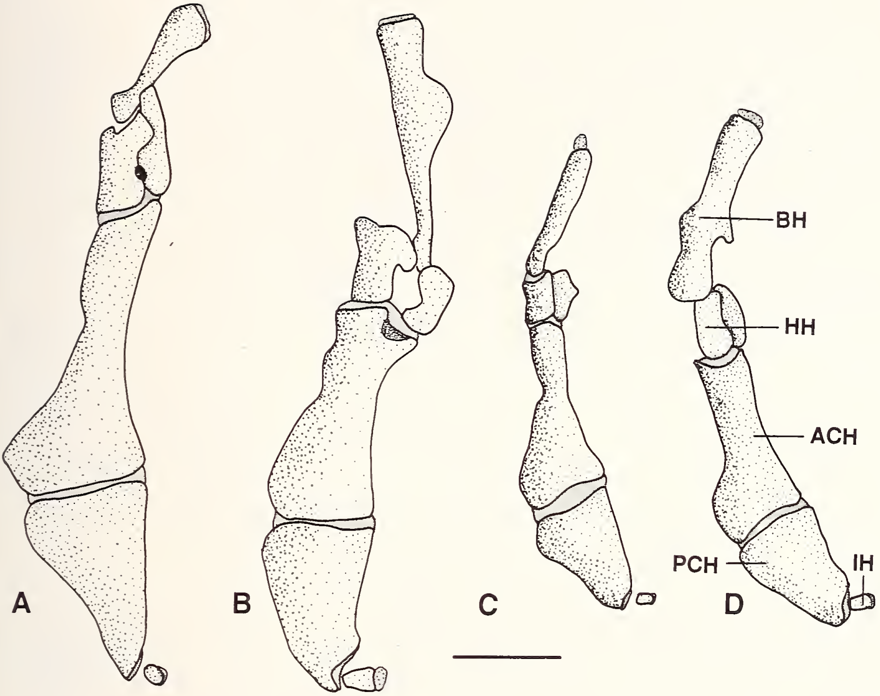

Fig.65: Lateral view of the hyoid arch and basihyal of *Phoxinus*. A: *P. neogaeus* (KU 8521, 53.0 mm SL); B: *P. phoxinus* (CNUC uncat., 76.0 mm TL); C: *P. eos* (KU 12255, 43.0 mm SL); D: *P. cumberlandensis* (KU 18934, 52.0 mm SL). Scale bars = 1 mm.

cies of the *Phoxinus* and in the outgroups (TS 114[0]). The anterior end of branchiostegal 3 is deeply concave in *P. issykkulensis* (TS 115[1]); the anterior end is not concave in other species of the genus and in the outgroups (TS 115[0]).

Interhyal (Figs.64A-E, 65A-D). The interhyal is a small paired bone located at the most posterior portion of the hyoid region. It articulates with the dorsal side of the posterior ceratohyal, and ventral side of the hyomandibula dorsally via cartilage attaching on the hyomandibula. No variation was found among *Phoxinus* species.

Posterior Ceratohyal (Figs.64A-E, 65A-D). In *Phoxinus*, the posterior ceratohyal is a triangular bone and articulates with the anterior ceratohyal anteriorly, and interhyal posterodorsally. The dorsal side of the posterior ceratohyal bears a notch with which the interhyal articulates. The bone is elongated triangular-shaped in *P. neogaeus, issykkulensis, brachyurus*, and *phoxinus* (TS 116 [1]), whereas it is short triangular-shaped in other species of *Phoxinus* (TS 116[0]) and in the outgroups.

Anterior Ceratohyal (Figs.64A-E, 66A-D). The anterior ceratohyal is the largest element in the hyoid region, and articulates with the ventral end of the posterior ceratohyal posteriorly, and (the dorsal and ventral) hypohyals anteriorly. The anterior ceratohyal is

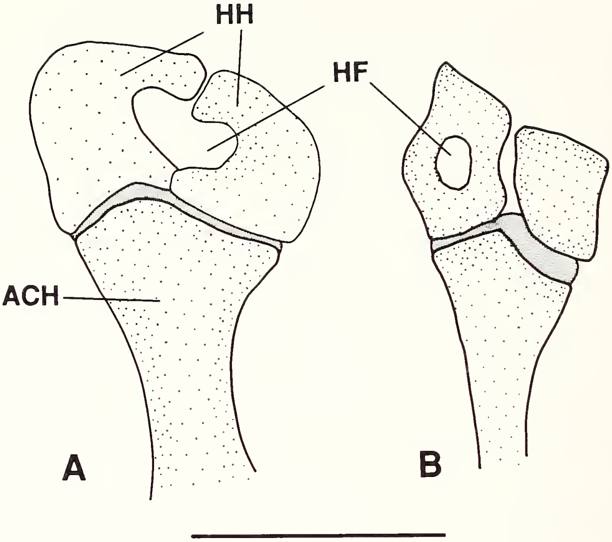

Fig.66: Anterior ceratohyal and hypohyals in lateral view of (A) *Phoxinus oreas* (KU 3259, 55 mm SL), and (B) *P. eos* (KU 12255, 43.0 mm SL). Scale bars = 1 mm.

elongated with a shallow constriction on its anterior portion; its posterior portion is broader than its anterior portion. The anterior margin of the bone is concave in *P. cumberlandensis* and *tennesseensis* (TS 117[1]); the margin is not concave in other species of *Phoxinus* (TS 117[0]) and in the outgroups. Moreover, a notch is present at the anterior margin of the anterior ceratohyal in *P. phoxinus* and *issykkulensis* (TS 118[1]). This notch is absent in other species of *Phoxinus* and in the outgroups (TS 118[0]).

Hypohyal (Figs.65A-D, 66A-B). In cyprinids, two hypohyals, i.e., dorsal and ventral ones (dorsohyal and ventrohyal in Howes 1978), are present at each side. The dorsal and ventral hypohyals are joined each other by ligaments (Howes 1978). The posterior side of the dorsal hypohyal contacts the dorsoanterior side of anterior ceratohyal, and the ventroposterior side of the ventral hypohyal articulates with the ventroanterior side of the anterior hypohyal. Both hypohyals articulate with the posterior side of the basihyal anteriorly.

In *Phoxinus*, the two hypohyals are not identical in shape. Generally, the bones are rectangular with a notch at the ventral side of the dorsal hypohyal, and a notch at the dorsal side of the ventral hypohyal. The hyoid foramen is usually formed between the two hypohyals (Fig.66A). This condition is present in all species of *Phoxinus*, except *P. eos*, and in the outgroups (TS 119[0]). In *P. eos*, the foramen is formed by the single ventral hypohyal (TS 119[1]) (Fig.66B). In *P. neogaeus*, a concavity is present at the dorsal side of the ventral hypohyal and the ventral side of the dorsal hypohyal (TS 120[1]) – an apomorphic condition found in this species only. In other *Phoxinus* and in the outgroups, the concavity is not present (TS120[0]).

Basihyal (Fig.65A-D). In cyprinids, the basihyal is a single bone located anterior to the hypohyal, and articulates with the left and right hypohyals posteriorly. It is rod- or bar-shaped. In *Phoxinus*, the middle of the lateral side of the basihyal is concave. In *P. cum-*

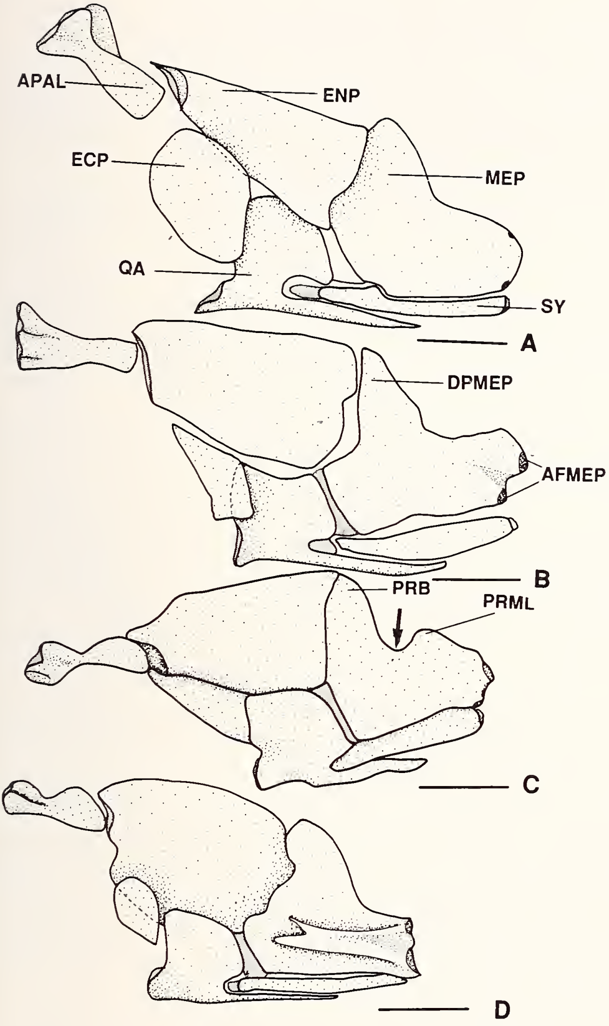

Fig.67: Lateral view of the suspensorium of *Phoxinus*. A: *P. tennesseensis* (UT 44.5274, 50.0 mm SL); B: *P. erythrogaster* (KU 5773, 51.5 mm SL); C: *P. phoxinus* (CNUC uncat., 76.0 mm TL); D: *P. eos* (KU 12255, 43.0 mm SL). The arrow shows notch of the metapterygoid; scale bars = 1 mm.

berlandensis, the anterior portion of the basihyal is bar-shaped, the posterior portion is plate-like with a fork at its lateral margin (TS 121[1]). In other species of *Phoxinus* and in the outgroups, the bone does not bear the fork (TS 121[0]).

Suspensorium

The lower jaw is suspended to the neucranium via the suspensorium. Bones included in the suspensorium are entopterygoid, ectopterygoid, autopalatine, quadrate, symplectic, metapterygoid, and hyomandibula. All are paired bones. Among them, the autopalatine, metapterygoid, hyomandibular, symplectic and quadrate are chondral bones; whereas, the entopterygoid and ectopterygoid are dermal elements (Arratia & Schultze 1991).

Entopterygoid (Figs.67A-D, 68A-D). In cyprinids, the entopterygoid is an irregularly shaped plate-like dermal bone and located anteriorly to the metapterygoid. It sutures with the anterior margin of the metapterygoid posteriorly, dorsal margin of the quadrate and ectopterygoid ventrally, and posterior end of the autopalatine anteriorly.

In *Phoxinus*, variations of the entopterygoid are in two aspects: the general shape and the articulation with the autopalatine. The entopterygoid is long (anterior-posterior dimension) and relatively narrow (ventral-dorsal dimension) in *P. issykkulensis, tennesseensis*, and *cumberlandensis* (TS 122[1]); whereas the bone is short and relatively broad in other species of *Phoxinus* (TS 122[0]). In *P. eos, erythrogaster*, and *phoxinus*, the entopterygoid articulates with the posterior end of autopalatine (TS 123[1]); in other species of *Phoxinus* and in the outgroups, it articulates with almost half of the autopalatine (TS 123[0]).

Ectopterygoid (Figs.67A-D, 68A-D). In cyprinids, the ectopterygoid is a small dermal bone placed at the anteroventral side of the entopterygoid. Its posterior side articulates with the anterior margin of the entopterygoid and the quadrate. The ectopterygoid is narrow, slender, and crescent in *P. neogaeus, issykkulensis, erythrogaster*, and *phoxinus* (TS 124[1]); it is relatively short and broad in other species of *Phoxinus* and in the outgroups (TS 124[0]). The ectopterygoid does not overlap the anterior portion of the entopterygoid in *P. erythrogaster, issykkulensis, phoxinus, tennesseensis*, and *cumberlandensis* (TS 125[1]); the ectopterygoid partially overlaps the entopterygoid in other species of *Phoxinus* and in the outgroups (TS 125[0]). The dorsal margin of the ectopterygoid is far away from the posterior end of the autopalatine in *P. tennesseensis, issykkulensis, neogaeus, erythrogaster, oreas, eos*, and in the outgroups (TS 126[0]); whereas the two bones are close to each other in other species of *Phoxinus* (TS 126[1]).

Autopalatine (Figs 67A-D, 68A-D). This small endochondral bone is located at the anterior portion of the suspensorium. The anterior portion of the autopalatine articulates with the supraethmoid via a ligament, and connects with the kinethmoid, vomer, maxilla, and infraorbital bone 1 anteriorly. The posterior portion of the autopalatine articulates with the anterior margin of the entopterygoid posteriorly. As discussed under "ectopterygoid," the relative position between the posterior end of the autopalatine and dorsal margin of the endopterygoid varies among the species of *Phoxinus*.

In *Phoxinus*, the autopalatine is a short bar-shaped bone with a forked structure at the anterior end. The shape of this forked structure shows intraspecific variation. Variation with phylogenetic significance includes two aspects. In *P. phoxinus, eos, cumberlandensis*, and *issykkulensis*, the autopalatine is short, slender, and not well-developed (TS 127[1]) when the similar sized specimens of other *Phoxinus* species and outgroups are compared (TS 127[0]). In *P. phoxinus* and *eos*, the dorsal and ventral margins are concave (TS 128[1]); the margins are almost straight in other species of *Phoxinus* and in the outgroups (TS 128[0]).

Quadrate (Figs.67A-D, 68A-D). In cyprinids, the quadrate is located ventral to the entopterygoid and anterior to the metapterygoid. It articulates with the symplectic dorsally, and with the anguloarticular ventroanteriorly.

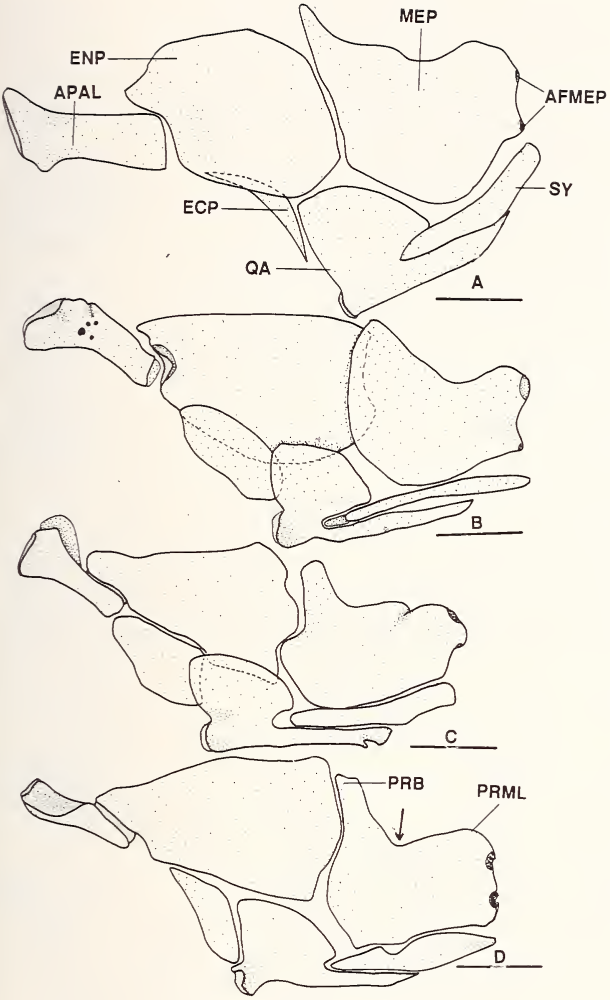

Fig.68: Lateral view of suspensorium *Phoxinus*. A: *P. neogaeus* (KU 8521, 53 mm SL); B: *P. oreas* (KU 3259, 55.0 mm SL); C: *P. cumberlandensis* (KU 18934, 52.0 mm SL); D: *P. issykkulensis* (P-10696, 42.4 mm SL). The arrow shows notch of the metapterygoid; scale bars = 1 mm.

The shape of the quadrate varies greatly in cyprinids. Generally, it is a square-shaped plate bone with a posterior process at its ventral portion, articulating with the symplectic and a condyle (or the articular facet, Arratia & Schultze 1991) at its anteroventral side that articulates with the anguloarticular. The quadrate can be high and short (e.g., *Moroco keumgang* – see Kim & Kang 1986), or low and elongated (e.g., *Luciobrama macrocephalus, Elopichthys bambusa* – see Howes 1978, Chen 1987b). The long and elongated condition is generally present in the fish with elongated neurocranium (Howes 1978, Chen 1987b). In *Luciobrama macrocephalus*, a foramen is present at the area posterior to the condyle of the quadrate (Howes 1978, Chen 1987b). Howes (1978:15) indicated that "there appears to be no nerve or vessel of any kind passing through this aperture but only fibers of the connective tissue which line the floor of the branchial cavity." This foramen has not been reported from other cyprinids.

In *Phoxinus*, the quadrate is high and short. The posteroventral side of the process, articulating with the symplectic, bears a notch in *P. cumberlandensis* (TS 129[1]), which is absent in other species of *Phoxinus* and in the outgroups (TS 129[0]).

Symplectic (Figs.67A-D, 68A-D). In cyprinids, the symplectic is an elongated rod-shaped bone and positioned ventral to the metapterygoid. The symplectic articulates with ventral margin of the metapterygoid dorsally, dorsal margin of the posterior process of quadrate ventrally, and ventral side of the hyomandibular posteriorly.

In *Phoxinus*, the shape and the articulation of the symplectic with other bones are similar to that in most cyprinids. In *P. eos, oreas*, and *tennesseensis*, the symplectic is much slender (TS 130[1]) than that in other species of *Phoxinus* and in the outgroups (TS130[0]).

Metapterygoid (Figs.67A-D, 68A-D). In cyprinids, the metapterygoid is a plate-like endochondral bone located anteriorly to the hyomandibula. It articulates with the ventroanterior margin of hyomandibula posteriorly, dorsal margin of the symplectic ventrally, posterior margin of endopterygoid and posterior margin of the quadrate anteriorly.

In *Phoxinus*, the metapterygoid is irregular in shape with two articular facets for the hyomandibula (Figs.67A-D, 68A-D). The dorsal margin of the metapterygoid bears a processus basalis (basal process) on its anterior portion, a processus metapterygoideus lateralis (lateral process) on its posterior portion, and a notch between the two processes. The tri-

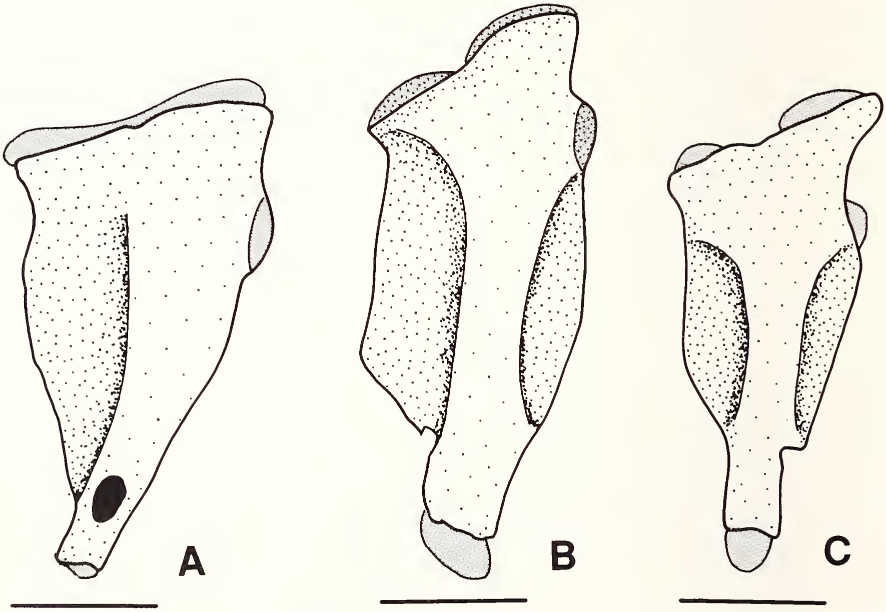

Fig.69: Lateral view of hyomandibula of *Phoxinus*. A: *P. issykkulensis* (P-10696, 42.4 mm SL); B: *P. cumberlandensis* (KU 18934, 52.0 mm SL); C: *P. eos* (KU 12255, 43.0 mm SL). Scale bars = 1 mm.

geminal nerve passes through the notch (Arratia & Schultze 1991). Variations of the metapterygoid include the relative position of the two articular surfaces at the posterior margin, and shape of the two processes.

The two articular surfaces at the posterior margin of the metapterygoid are well-developed and close to each other in *P. eos, brachyurus, issykkulensis, erythrogaster*, and *phoxinus* (TS 131[1]). In other species of *Phoxinus* and in the outgroups, the two surfaces are less developed (TS 131[0]).

The notch at the dorsal margin of the metapterygoid is deep in *P. brachyurus, phoxinus*, and in the outgroups (TS 132[0]); it is relatively shallow in other species (TS 132[1]).

The processus basalis of the metapterygoid is narrow and high in *P. erythrogaster, phoxinus, issykkulensis, cumberlandensis*, and in the outgroups (TS 133[0]); the process is broad and relatively lower in other species of *Phoxinus* (TS 133[1]).

Hyomandibular (Figs.69A-C, 70A-F). In cyprinids, the hyomandibular is an endochondral bone and is placed at the posterior portion of the viscerocranium. The dorsal

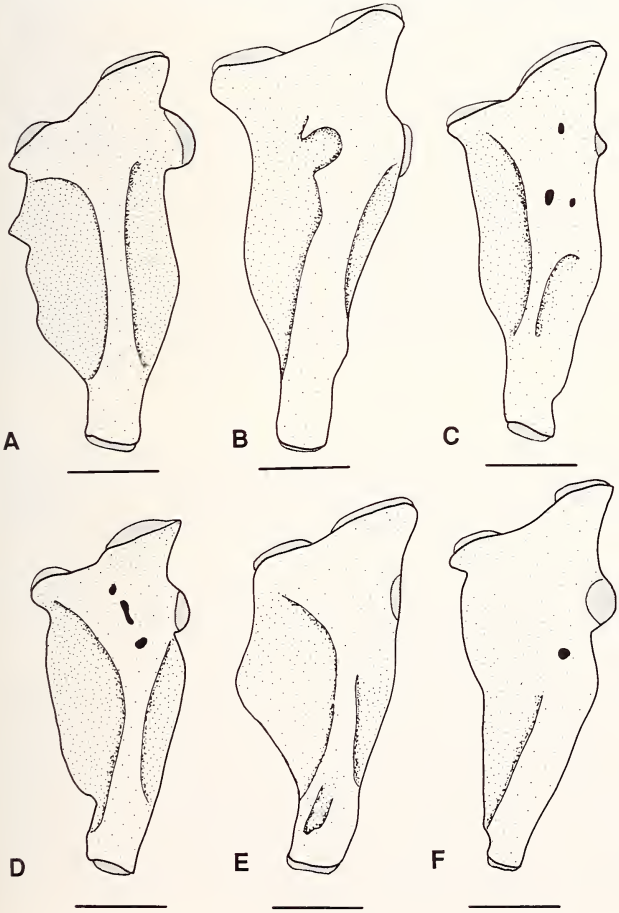

Fig.70: Lateral view of hyomandibula of *Phoxinus*. A: *P. phoxinus* (CNUC uncat., TL 76.0 mm); B: *P. neogaeus* (KU 8521, 53.0 mm SL); C: *P. oreas* (KU 3259, 55.0 mm SL); D: *P. erythrogaster* (KU 5773, 51.5 mm SL); E: *P. brachyurus* (MCZ 3006, 75.9 mm SL); F: *P. tennesseensis* (UT 44.5274, 50.0 mm SL). Scale bars = 1 mm.

portion of the hyomandibula is broader than the rest of the bone. The dorsal margin of the bone is concave and thus forms two articular facets. The anterior facet contacts the hyomandibular fossa which is formed by the sphenotic, pterosphenoid, and the prootic; the posterior one fits into the hyomandibular fossa that is formed by the sphenotic, prootic, and pterotic (Howes 1978, Arratia & Schultze 1991).

The dorsoposterior margin of the hyomandibular bears an articular facet, articulating with the anterior margin of the opercle. The ventral margin of the hyomandibular contacts the dorsoposterior end of the symplectic, and the anterior margin contacts the surfaces at the posterior margin of the metapterygoid.

In *Phoxinus*, the hyomandibular is a plate-like bone. As in other cyprinids, two articulating facets are present on its dorsal margin. The hyomandibular is thick at its dorsal and middle part: it is thin at its anteroventral and posteroventral part. Therefore, three parts can be recognized from the bone, i.e., the body (the thick part), the anterior wing (the anterior thin part), and the posterior wing (the posterior thin part).

The hyomandibular is broad and relatively short in *P. brachyurus, phoxinus*, and *issykkulensis* (TS 134[0]). It is narrow and relative long in other *Phoxinus* species (TS134[1]). The bone bears a notch at the ventroanterior margin in *P. cumberlandensis* and *erythrogaster* (TS 135[1]); the notch is absent in other species of *Phoxinus* (TS 135[0]). In *P. eos*, a notch is present at the ventroposterior margin of the hyomandibular (TS 136[1]); this notch is absent in other *Phoxinus* species (TS 136[0]).

A cartilage is present at the ventral end of the hyomandibula, articulating with the symplectic. The cartilage is large in *P. cumberlandensis, erythrogaster*, and *eos* (TS 137[1]); it is much smaller in other species of *Phoxinus* (TS 137[0]).

In the outgroups, the short and relatively broad hyomandibula does not bear notches at its ventroanterior and ventroposterior margins. A small cartilage is attatched to the ventral end of the bone.

Opercular Region

In cyprinids, the opercular region is located at the most posterior portion of the viscerocranium, and forms the lateral cover for the gill arches. It is composed of four dermal paired plate bones, i.e., the opercular, subopercular, interopercular, and preopercular bones.

Opercle (Figs.71A-F). The opercle is the largest bone in the opercular region and slightly square-shaped in *Phoxinus*. The opercle articulates with the hyomandibula and preopercle anteriorly, the interopercle ventroanteriorly, and the subopercle ventrally.

The shape of the opercle varies among species of *Phoxinus*. It is elongated and narrow in *P. cumberlandensis* (TS 138[1]); it is short and broad in other *Phoxinus* species (TS 138[0]). The dorsal margin of the bone is almost straight in *P. brachyurus, tennesseensis*, and *cumberlandensis* (TS 139[0]); the margin is concave in *P. erythrogaster, oreas, eos, neogaeus, issykkulensis*, and *phoxinus* (TS 139[1]). A narrow and sharp anterodorsal process is present at the anterior end of the dorsal margin in *P. cumberlandensis, tennesseensis, oreas, neogaeus*, and *phoxinus* (TS 140[1]); the process is broad and blunt in *P. erythrogaster, eos, brachyurus*, and *issykkulensis* (TS 140[0]).

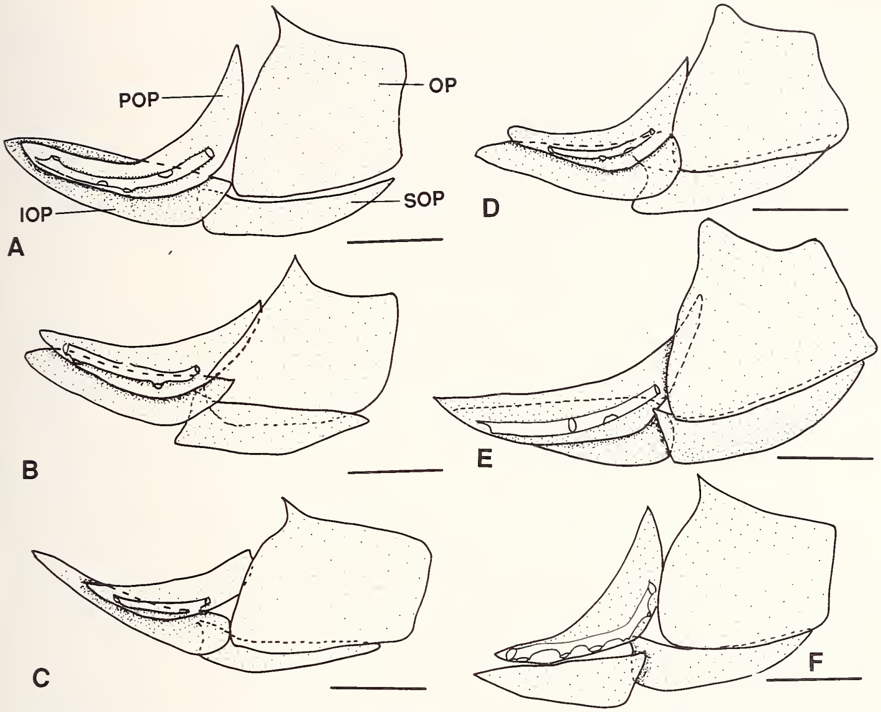

Fig.71: Lateral view of the opercular series of *Phoxinus*. A: *P. tennesseensis* (UT 44.5274, 50.0 mm SL); B: *P. phoxinus* (KU 22856, 56.0 mm SL); C: *P. cumberlandensis* (KU 18934, SL 54.3 mm SL); D: *P. eos* (KU 12255, 43.0 mm SL); E: *P. issykkulensis* (P-10696, 42.4 mm SL); F: *P. oreas* (KU 3259, 52.2 mm SL). Scale bars = 1 mm.

Interopercle (Figs.71A-F). The interopercle is placed at the anteroventral portion of the opercular series. It is partially overlapped by ventral side of the preopercle dorsally, and by anterior portion of the subopercle posteriorly.

The interopercle is elongated triangular plate-like and tapes anteriorly; therefore, its anterior portion is narrower than its posterior portion. The shape of its posterior margin varies individually. The posterior margin can be concave, slope, or round in different specimens of a single species.

Preopercle (Fig.71A-F). The preopercle is a "L"-shaped bone and located anteriorly to the opercle. Its posterior portion contacts the anterior margin of the opercle, its ventral margin contacts with dorsal side of the interopercle. It is crescent in shape, and its middle portion is broader than its anterior and dorsal portions. No variation with phylogenetic significance is observed in *Phoxinus*.

Subopercle (Fig.71A-F). Placed ventrally to the opercle, the subopercle contacts the opercle dorsally and the preopercle anteriorly.

In *Phoxinus* the subopercle is an elongated triangular bone; thus three angles can be recognized, i.e., the anterodorsal, anteroventral, and posterior angles. The subopercle is broader at its anterior portion than at its posterior portion. The dorsal and ventral margins of the bone are much longer than the anterior margin. The posterior angle is elongated and blunt. The anterodorsal angle might be acute or blunt with intraspecific variation. The anteroventral angle is blunt. In *P. neogaeus, issykkulensis*, and *tennesseensis*, the anterior margin of the bone is straight (TS 141[1]); in other species of *Phoxinus* and in the outgroups, the margin is concave (TS 141[0]).

Branchial Region

Bones included in the branchial region are pharyngobranchials, epibranchials, ceratobranchials, hypobranchials, basibranchials, and pharyngeal bones. These bones form the gill arch. They can be grouped into two sets, i.e., the dorsal and ventral elements. The dorsal elements include epibranchials and pharyngobranchials, both of which are suspended on the ventral aspect of neurocranium. The ventral elements include rest of the bones.

Pharyngobranchials (PHB, Fig.72A-F). In cyprinids, the pharyngobranchials are placed at the dorsomedial portion of the gill arches and contact the ventral side of the parasphenoid. There are four paired elements, i.e., pharyngobranchials 1, 2, 3, and 4 (from anterior to posterior). Pharyngobranchials 2 and 3 are fused in cyprinids (Chen 1986b, Mayden 1989); whereas the pharyngobranchial 4 is a cartilage present in some species only (e.g., *Luciobrama macrocephalus* – see Howes 1978). Howes (1978) and Kim & Kang (1986) recognized the two pharyngobranchials (PHB 1, and 2+3 herein) in cyprinids (their infrapharyngobranchials) as the pharyngobranchials 2 and 3, the cartilage in front of the first pharyngobranchial was interpreted as the pharyngobranchial 1.

In *Phoxinus*, pharyngobranchial 1 (Fig.72A-F) articulates with epibranchials 1 and 2 laterally, and pharyngobranchial 2+3 posteriorly. The bone is crescent and shallowly concave at its medial margin. The anterior portion of the pharyngobranchial 1 is broader than the posterior portion of the bone, its posterior margin is not forked in *P. brachyurus, phoxinus, neogaeus, eos, tennesseensis, oreas, cumberlandensis*, and *erythrogaster* (TS 142[0]); especially in *P. neogaeus*, the anterior portion of the bone is much broader than its posterior portion, and the bone is wedge-shaped. In *P. issykkulensis*, the posterior portion of the pharyngobranchial 1 is broader than the anterior portion of the bone, its posterior margin is deeply forked (TS 142[1]).

In the outgroups, the pharyngobranchial 1 is crescent, the anterior portion is broader than the posterior portion, its posterior margin is not forked.

Pharyngobranchial 2+3 (Fig.72A-F) is an elongated bone; it is larger than, and located posteriorly to pharyngobranchial 1. It articulates with pharyngobranchial 1 anteriorly, epibranchials 2 and 3 laterally, and pharyngobranchial 4, if any, posteriorly.

Pharyngobranchial 2+3 is crescent-shaped in *P. eos, oreas, erythrogaster, tennesseensis*, and *cumberlandensis* (TS143[1]). The bone bears a concavity at its lateral and medial sides, the posterior portion of the bone is generally broader than the anterior portion in *P. neogaeus, phoxinus, brachyurus, issykkulensis*, and the outgroups (TS 143[0]). In *P. neogaeus*, the concavity is not well developed.

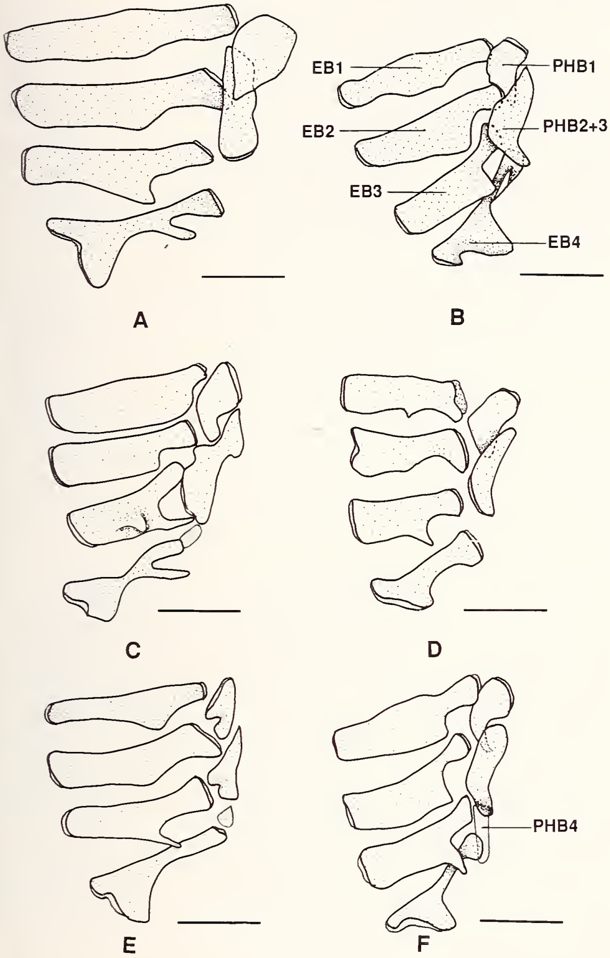

Fig.72: Dorsal view of pharyngobranchials and epibranchials of *Phoxinus*. A: *P. neogaeus* (KU 8521, 53.0 mm SL); B: *P. erythrogaster* (KU 5773, 51.5 mm SL); C: *P. phoxinus* (CNUC uncat., 76.0 mm TL); D: *P. eos* (KU 11335, 49.0 mm SL); E: *P. issykkulensis* (P-10696, 42.4 mm SL); F: *P. oreas* (KU 3259, 55.0 mm SL). Scale bars = 1 mm.

Pharyngobranchial 4 (Fig.72A-F) is a cartilage in *Phoxinus*, and placed at the posterior margin of the pharyngobranchial 2+3. It contacts the pharyngobranchial 2+3 anteriorly, and epibranchial 4 posteriorly. This cartilage is a slender bar in shape. Pharyngobranchial 4 is present in *P. oreas, issykkulensis*, and *phoxinus* (TS 144[1]), but absent in other species of *Phoxinus* and in the outgroups (TS 144[0]).

Epibranchials (Fig.72A-F). Four paired bones are included, i.e., epibranchials 1, 2, 3, and 4.

Epibranchial 1 (Fig.72A-F) is a bar-shaped bone articulating with pharyngobranchial 1 dorsally, and ceratobranchial 1 ventrally. The dorsal portion of epibranchial 1 is narrower than the ventral portion. In *P. erythrogaster, phoxinus, issykkulensis*, and *oreas*, the dorsal portion of epibranchial 1 is constricted, much narrower than the ventral portion of the bone (TS 145[1]). This condition is not present in other species of *Phoxinus* or the outgroups (TS 145[0]).

Epibranchial 2 (Fig.72A-F) articulates with pharyngobranchials 1 and 2+3 dorsally, and ceratobranchial 2 ventrally. It is short, bar-shaped and has a concavity at its dorsoanterior and dorsoposterior margins. In *P. erythrogaster, phoxinus*, and *oreas*, the dorsal portion of the bone is constricted (TS 146[1]). This condition is not present in other species of *Phoxinus* or in the outgroups (TS 146[0]). The ventral margin of the epibranchial 2 is deeply concave in *P. eos* (TS 147[1]); the margin is not concave in other *Phoxinus* species or in the outgroups (TS 147[0]).

Epibranchial 3 (Fig.72A-F) articulates with pharyngobranchial 2+3 dorsally, and ceratobranchial 3 ventrally. It is bar-shaped and forked at its dorsal portion. In *Phoxinus neogaeus, eos, cumberlandensis, erythrogaster, tennesseensis, brachyurus, oreas*, and *issykkulensis*, the posterior process of the dorsal forked structure is much shorter than the anterior branch (TS 148[0]). In *P. phoxinus*, the posterior process is of the same length as the anterior one (TS 148[1]). Therefore, two articular condyles to the pharyngobranchial 2+3 are formed in *P. phoxinus*. Moreover, there is a posterior process at the middle of the bone's lateral side in *P. phoxinus* (TS 149[1]). The process is absent in other species of *Phoxinus* and in the outgroups (TS 149[0]).

Epibranchial 4 (Fig.72A-F) articulates with pharyngobranchial 4 (if any) dorsally, and ceratobranchial 4 ventrally. In *Phoxinus*, this bone is bar-shaped with constriction at the middle of its anterior and posterior margins. The ventral margin of epibranchial 4 is straight in *P. eos, tennesseensis, oreas*, and *cumberlandensis* (TS 150[0]); it is deeply concave, with two articulating facets contacting the dorsal side of ceratobranchial 4 in *P. erythrogaster, neogaeus, brachyurus, phoxinus*, and *issykkulensis* (TS 150[1]). The dorsal margin of epibranchial 4 is deeply concave in *P. neogaeus* and *phoxinus* (TS 151[1]); the margin is straight without concavity in other species of *Phoxinus* (TS 151[0]) and in the outgroups. The posterior margin of epibranchial 4 bears a wide notch in *P. cumberlandensis, issykkulensis, oreas, erythrogaster, tennesseensis, brachyurus, eos*, and in the outgroups (TS 152[0]); the posterior margin is deeply concave in *P. neogaeus* and *phoxinus* (TS 152[1]).

In *P. erythrogaster* and *P. brachyurus*, a dorsally directed elongated process is present at the lateral side of epibranchial 4 (TS 153[1]). This process is absent in other species of *Phoxinus* and in the outgroups (TS 153[0]).

Ceratobranchials (Fig.73A-F). The ceratobranchials are the longest elements in the branchial region, and consists of four pairs of bones, i.e., ceratobranchials 1, 2, 3, and 4. All ceratobranchials are elongated bar-shaped and bear cartilage at both dorsal and ventral ends. Each ceratobranchial articulates with the same numbered epibranchial dorsally and same numbered hypobranchial ventrally, except ceratobranchial 4 because hypobranchial 4 is absent. No variations with phylogenetic significance are present among the species of *Phoxinus*.

Hypobranchials (Fig.73A-F). Three paired small hypobranchials (1, 2 and 3) are present in *Phoxinus*; they articulates with the same numbered ceratobranchials laterally.

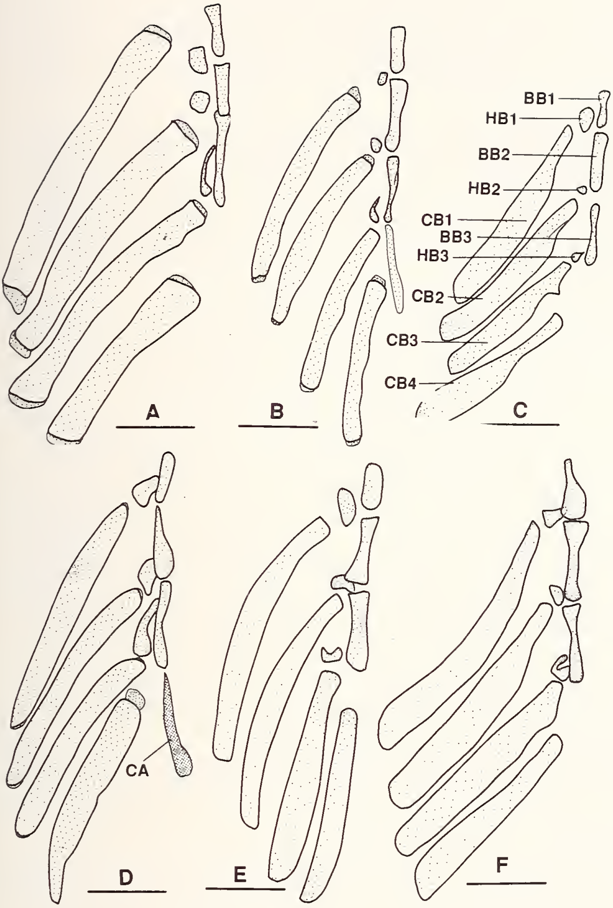

Fig.73: Dorsal view of ceratobranchials, hypobranchials, and basibranchials of *Phoxinus*. A: *P. phoxinus* (CNUC uncat., 76.0 mm TL); B: *P. eos* (KU12255, 43.0 mm SL); C: *P. cumberlandensis* (KU 18934, 52.0 mm SL); D: *P. issykkulensis* (P-10696, 42.4 mm SL); E: *P. oreas* (KU 3259, 55.0 mm SL); F: *P. erythrogaster* (KU 5773, 51.5 mm SL). Scale bars = 1 mm.

Hypobranchials 1 and 2 (Fig.73A-F) are small bones. No variation with phylogenetic significance is present among *Phoxinus* species.

Hypobranchial 3 (Fig.73A-F) is a slender bone tapering ventrally. The left and right hypobranchials 3 are close to each other at their ventral ends, forming an arch-like structure. Basibranchial 3 runs through the arch (Chen 1986b). Variation exists in size of the hypobranchial 3 relative to the basibranchial 2. In *P. phoxinus* and *issykkulensis*, hypobranchial 3 is elongated and its length is almost equal to that of basibranchial 2 (TS 154[1]). In other species of *Phoxinus*, this bone is much shorter than that of basibranchial 2 (TS 154[0]), which is similar to the condition in the outgroups.

Basibranchials (Fig.73A-F). Bones included are three single basibranchials (1, 2 and 3, from anterior to posterior) and placed mesially between the right and left hypobranchials.

In all *Phoxinus* species and in the outgroups, except *P. erythrogaster*, basibranchial 1 (Fig.75A-F) is bar-shaped and slightly concave at the lateral margin (TS 155[0]). In *P. erythrogaster*, the basibranchial 1 is wedge-shaped and its anterior portion is narrower than its posterior portion (TS 155[1]).

Basibranchial 2 (Fig.73A-F) articulates with the posterior margin of basibranchial 1 anteriorly, the anterior margin of the basibranchial 3 posteriorly, and the medial margin of hypobranchial 1 and 2 laterally. It is a slender bar-shaped bone with a slightly concave lateral side. The anterior and posterior ends are broader than the middle of the bone in all *Phoxinus* species and in the outgroups (TS 156[0]), except *P. issykkulensis* in which the bone is tapering anteriorly and sharp at the anterior end (TS 156[1]).

Similar to basibranchials 1 and 2 described above, basibranchial 3 (Fig.73A-F) articulates with the posterior end of basibranchial 2 anteriorly, mesial of hypobranchial 2 and 3 anterolaterally and posteriorly respectively. It is also similar to the basibranchial 2 in shape. It varies in size relative to the basibranchial 2. It is much longer (about two times) than the basibranchial 2 in *P. phoxinus* (TS 157[1]); it is almost of the same length of the basibranchial 2 in other species of *Phoxinus* and the outgroups (TS 157[0]).

In *P. neogaeus, eos*, and *issykkulensis*, an elongated cartilage is present at the posterior end of basibranchial 3 which articulates with ventral side of the epibranchial 4 (TS 158[1]). The cartilage is less developed in *P. neogaeus* than that in *P. issykkulensis* and *eos*. The cartilage is very small in other species of *Phoxinus* and the outgroups (TS 158[0]).

Pharyngeal bones and pharyngeal teeth (Fig.74A-C). The pharyngeal bones bearing pharyngeal teeth are located posteriorly to the forth gill arch. It is the fifth ceratobranchial (Gasowska 1979, Chen 1986b). In cyprinids, the shape of the pharyngeal bones shows a great variation, from very slender (e.g., *Erythroculter ilishaeformis* – Yi & Wu 1964) to very broad (e.g., *Cyprinus carpio*). The pharyngeal teeth on the pharyngeal bone vary in rows and shape in cyprinids. One (e.g., *Rhodeus sericeus*), two (e.g., *P. phoxinus*), three (e.g., *Schizothorax prenanti*), even four rows (*Tetrostichodon* – see Cao 1964) of pharyngeal teeth are present in cyprinids. The teeth vary from slender (e.g., *Acanthorhodeus peihoensis*) to strong (e.g., *Mylopharyngodon piceus*). Almost no book or paper on the taxonomy of cyprinids does not consider the pharyngeal bone and teeth as some of the most useful characters in the identification of genera or species within the family (e.g., Nichols 1943, Wu 1964, 1977). The phylogenetic significance of the pharyngeal bone and the teeth of cyprinids has been discussed by many ichthyologists (e.g., Jurine 1821, Koh 1931, Chu 1935, Girgis 1952, Nikolsky 1963, Peyer 1963, Eastman 1970, Chen 1986a, 1987a, b). Jurine (1821) was the first one describing the pharyngeal bone and teeth of minnows (*Cyprinus carpio*). Chu (1935) was credited as the first known to study the pharyngeal bones and teeth of cyprinid systematically. Eastman & Underhill (1973) studied the intraspecific variation of the pharyngeal tooth formula.

The terms used herein for pharyngeal bones and teeth follow Chu (1935) and Eastman (1970), except the meaning of the posterior angle. The posterior angle (Fig.74) used herein is the angle between the main span of the posterior limb and the posterior edentulous process (Fig.74).

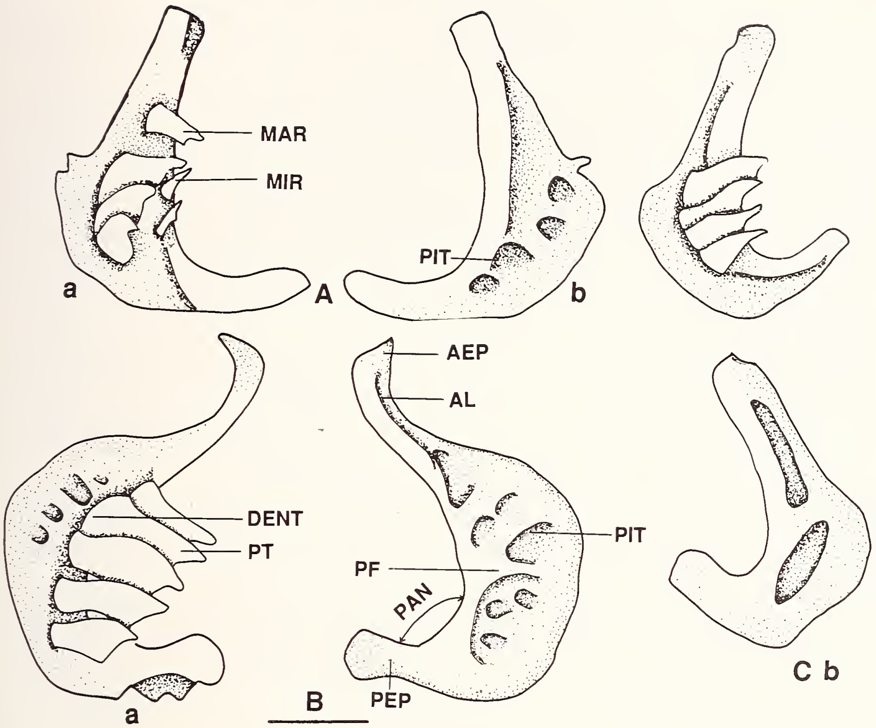

Fig.74: Pharyngeal bone and its teeth of *Phoxinus* in lateral (a) and dorsal (b) views. A: *P. phoxinus* (CNUC uncat. 76.0 mm TL); B: *P. cumberlandensis* (KU 18934, 52.0 mm SL); C: *P. eos* (KU 12255, 43.0 mm SL). Scale bars = 1 mm.

Generally, the pharyngeal bone in *Phoxinus* is "L"-shaped with expansion at the middle of its ventral side. The expanded ventral surface bears several pits, to which masticatory muscles are attached. These pits are well developed in *Phoxinus*. The pharyngeal teeth are located at the dentigerous surface. The teeth are dorsally directed and function to chew food with masticatory pad attached on the pharyngeal pad of the basioccipital bone.

Variations with phylogenetic significance including a few aspects of the pharyngeal bone and teeth among *Phoxinus* species can be described as follows (Fig.74A-C):

1. Posterior angle: This angle partially represents relationship between the posterior edentulous process and the main span of the posterior limb. The smaller the angle, the more anteriorly the posterior edentulous process bends. The angle is smaller in *P. eos, tennesseensis*, and *oreas* (TS 159[1]) than in other species of *Phoxinus* and in the outgroups (TS 159[0]).
2. Posterior edentulous process: The posterior edge of the posterior edentulous process bears a flat plate-shaped structure with two small processes in *P. cumberlandensis* (TS 160[1]) (Fig.74B); the structures is not present in other species of *Phoxinus* or in the outgroups (TS 160[0]).

3. Anterior edentulous process: The process is straight in *P. neogaeus, erythrogaster, phoxinus*, and *eos* (TS 161[1]); it is bent in other species of *Phoxinus* and in the outgroups (TS 161[0]).

4. Tip of the anterior limb: A notch is present at tip of the anterior limb in *P. issykkulensis* and *P. eos* (TS 162[1]); this notch is not present in other species of *Phoxinus* or in the outgroups (TS 162[0]).

5. Pitted surface: Different numbers of pits are present on the surface. Generally, there are a few large and numerous small pits, such as in *P. brachyurus, issykkulensis, oreas, phoxinus, neogaeus, tennesseensis, cumberlandensis*, and in the outgroups (TS 163[0]). In *P. eos*, and *erythrogaster*, however, only two or three large and elongated pits are present with very few or without small ones (TS 163[1]).

6. Pharyngeal teeth: The pharyngeal teeth are present in one row in all North American *Phoxinus* (TS 164[1]) except *P. neogaeus*; the teeth are in two rows in all Eurasian *Phoxinus* (*P. phoxinus, brachyurus*, and *issykkulensis*) and the North American *P. neogaeus* (TS 164[0]). If two rows are present, the teeth on the main row are much higher, stronger, and better developed than that in the secondary (minor) row.

Two rows of pharyngeal teeth are present in the outgroups. The presence of one row of the teeth is therefore interpreted as apomorphic, and the presence of two rows of teeth as plesiomorphic in *Phoxinus*.

In the species with two rows of teeth, the formulae of the teeth usually are 5.2(1)-(1)2.5, or 4.2(1)-2(1).4. In the species with one row, the formulae generally are 5-5, or 4-4. However, intraspecific variation of the formulae is very common in *Phoxinus* (e.g., *P. phoxinus*), as indicated in "Species Account".

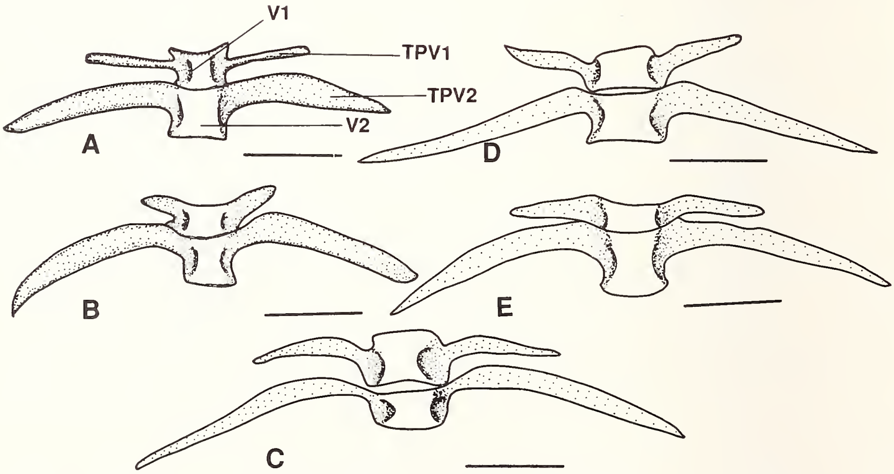

Fig.75: Ventral view of the first and second vertebrae of *Phoxinus*. A: *P. eos* (KU 12255, 43.0 mm SL); B: *P. cumberlandensis* (KU 18934, 52.0 mm SL); C: *P. neogaeus* (KU 8521, 53.0 mm SL); D: *P. oreas* (KU 3259, 55.0 mm SL); E: *P. erythrogaster* (KU 5773, 51.5 mm SL). Scale bars = 1 mm.

Vertebral Column

Weberian Apparatus. In cyprinids, the Weberian apparatus is located at the anterior vertebral column, and function as an otophysic connection between the anterior chamber of gas bladder and inner ear; thus, it can transmit movements of the gas bladder wall to the ear, and aid in hearing and depth perception (Alexander 1962). Two divisions can be recognized from the Weberian apparatus, the pars sustentaculum and the auditum. The pars sustentaculum is composed of the modified first four vertebrae, their arches and gas bladder, and partially function as a supporter for the pars auditum. The pars auditum consists of four paired Weberian ossicles, i.e., claustrum, scaphium, intercalarium, and tripus (from anterior to posterior). The ossicles form a bony chain, connected by ligaments between the ossicles, to connect the gas bladder and inner ear, and to function (with the related ligaments) as a medium to pass the information from the gas bladder to the ear. Numerous papers on the Weberian apparatus in cyprinids have been published. Watson (1939), Alexander (1962), Rosen & Greenwood (1970), and Fink & Fink (1981) are only a few important examples.

The Weberian apparatus in *Phoxinus* is similar to that in other cyprinids. In *Phoxinus*, the vertebral centrum (Figs 75A-E, 76A-D) is short with a short transverse process laterally (transverse process 1). Anteriorly, it articulates with the proatlas of the basioccipital bone. The scaphium and claustrum are placed at the dorsolateral side of the centrum. Variations in *Phoxinus* include the length and relative position of the transverse process. The transverse process is at the anterior margin of the vertebral centrum in *P. cumberlandensis, erythrogaster, tennesseensis*, and *phoxinus* (TS 165[1]). The transverse process is located at the middle of the lateral side of the vertebral centrum in other species and in the outgroups (TS 165[0]). The transverse process is very short, and extends only to the base of the transverse process of vertebra 2 (transverse process 2) in *P. cumberlandensis* (TS 166[1]). The transverse process is much longer, and almost equals about half of transverse process 2 in length in all other species of *Phoxinus* and in the outgroups (TS 166[0]).

The second vertebral centrum (Figs 75A-E, 76A-D, 77A-C) is more developed than the first one. Its transverse process is elongated. The intercalarium is located at the lateral side of the centrum. A developed neural arch (neural arch 2) is located at the dorsal side of the centrum, and is more or less semi-round. In *P. erythrogaster*, neural arch 2 bears an ascending process at its dorsal portion (TS 167[1]) that is absent in other species of *Phoxinus* and in the outgroups (TS 167[0]).

The third vertebral centrum is more developed than the previous two. No transverse process is present on vertebra 3. Ventrally, a notch is present at the lateral side of the centrum holding the medial ramus of the tripus. A developed neural arch is present at the centrum's dorsal side. Articulating with the ventral portion of neural arch 2 and the neural complex dorsally, neural arch 3 is irregularly shaped and bears an anterior process and a posterior notch. The process is narrow and relatively long in *P. phoxinus* (TS 168[1]; Fig.77A); the process is broad and relatively short in all other species of *Phoxinus* and in the outgroups (TS 168[0]).

The fourth vertebral centrum (Figs 76A-D, 77A-C, 78A-C) is of similar size to that of the third centrum. A well-developed rib (rib 4) is located at the centrum's lateral side. The

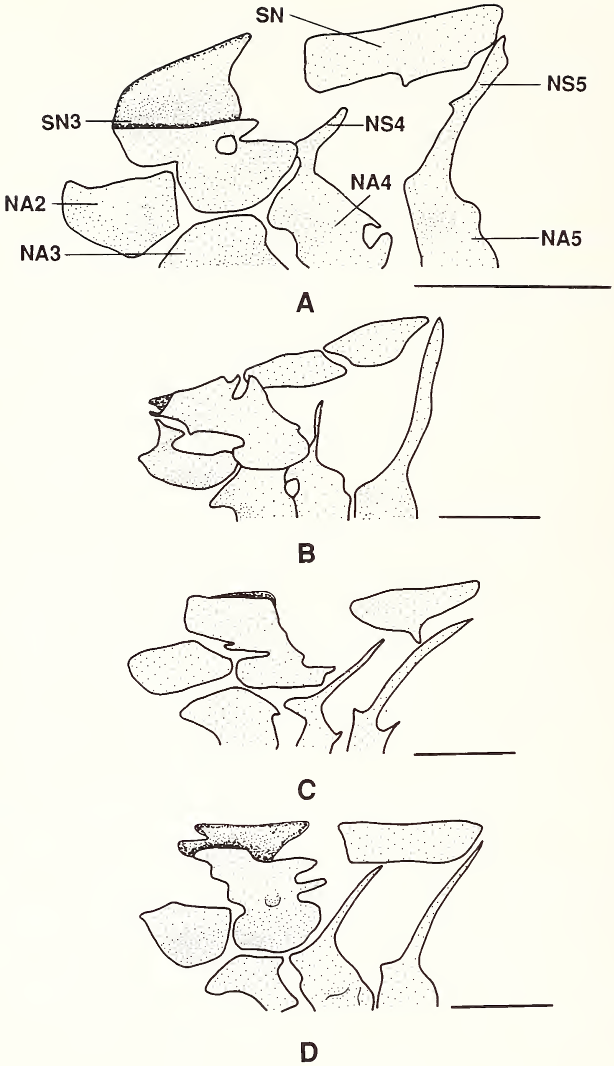

Fig.76: Lateral view of neural arches and spines of anterior vertebrae, neural complex, and supraneural bones of *Phoxinus*. A: *P. issykkulensis* (P-10696, 42.4 mm SL); B: *P. erythrogaster* (KU 5773, 51.5 mm SL); C: *P. neogaeus* (KU 8521, 53.0 mm SL); D: *P. tennesseensis* (UT 44.5274, 50.0 mm SL). Scale bars = 1 mm.

base of the rib is expanded, but the rib's ventral end is sharp. The rib bears a large and shallow notch at its median side in *P. eos* (TS 169[1]; Fig.77A); the notch is absent in other species of *Phoxinus* and in the outgroups (TS 169[0]).

The os suspensorium is developed and plate-like. The left and right os suspensoria are not fused mesially, and a space exists between the dorsal margin of the os suspensorium and the centrum of vertebra 4. The ventral end of the os suspensorium is at the same level of the ventral end of rib 4. Variation occurs in several aspects of the os suspensorium in *Phoxinus*. The os suspensorium is narrow in *P. tennesseensis, neogaeus, erythrogaster, eos,*

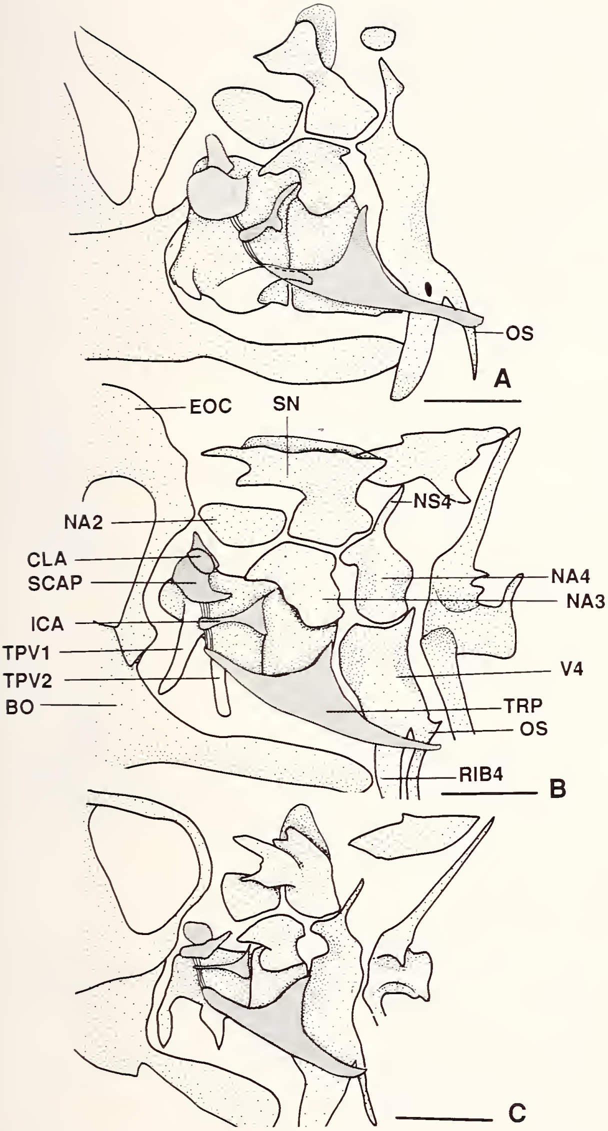

Fig.77: Lateral view of Weberian ossicles, anterior vertebrae and supraneural bones of *Phoxinus*. A: *P. phoxinus* (MCZ 32372, 72.0 mm SL); B: *P. cumberlandensis* (KU 18934, 52.0 mm SL); C: *P. eos* (KU 12255, 43.0 mm SL). Scale bars = 1 mm.

oreas, issykkulensis, brachyurus, phoxinus, and in the outgroups (TS 170[0]); it is broad in *P. cumberlandensis* (TS 170[1]). A notch is present at the medial margin of the suspensorium in *P. erythrogaster* and *P. eos* (TS 171[1]); the notch is absent in other species of *Phoxinus* and in the outgroups. A space from the dorsal margin to the ventral end of the os suspensorium is present between the left and right os suspensoria in *P. tennesseensis, neogaeus, erythrogaster, eos, issykkulensis, brachyurus, oreas, cumberlandensis*,

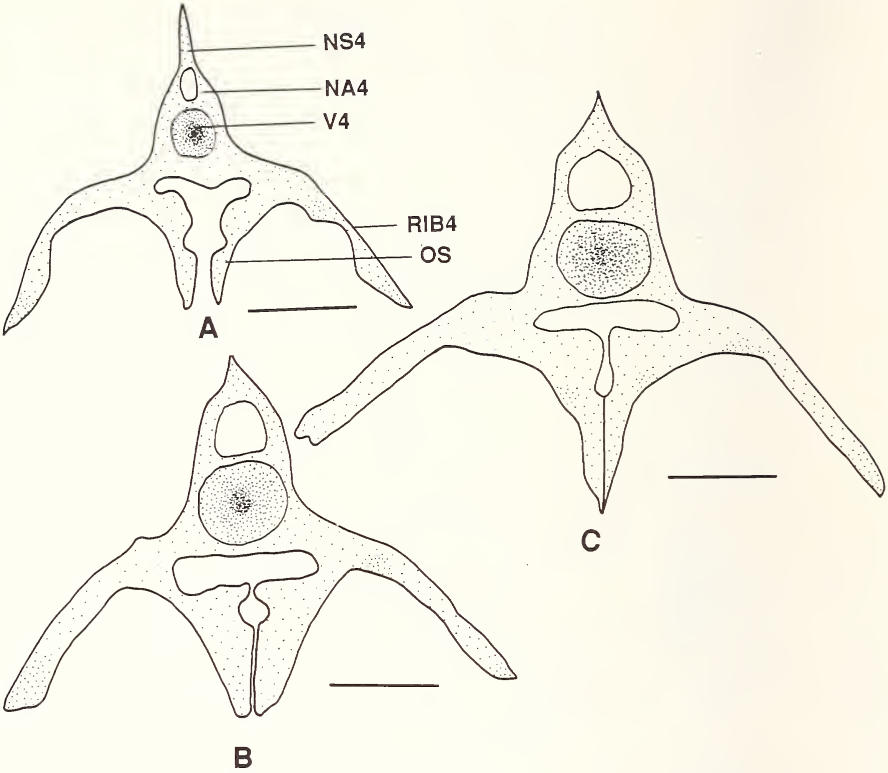

Fig.78: Posterior view of the fourth vertebra, and os suspensorium of *Phoxinus*. A: *P. eos* (KU 12255, 43.0 mm SL); B: *P. cumberlandensis* (KU 18934, 52.0 mm SL); C: *P. phoxinus* (CNUC uncat., 76.0 mm TL). Scale bars = 1 mm.

and in the outgroups (TS 172[0]); the space extends only to the middle of os suspensorium, the left and right parts of the os suspensorium contact each other at the medial from the middle to the ventral end of the os suspensorium in *P. phoxinus* (TS 172[1]).

A neural arch (neural arch 4) and spine are present on dorsal aspect of centrum 4. The anterior edge of neural arch 4 bears a notch. The notch is deep in *P. oreas, erythrogaster, eos*, and in the outgroups (TS 173[0]), but shallow in other species of *Phoxinus* (TS 173[1]). A space is present between the anterior margin of neural arch 4 and the posterior margin of neural arch 3. This space is partially formed by the notches at the anterior margin of the neural arch 4 and the posterior margin of the neural arch 3. The space extends only to the middle of the anterior margin of neural arch 4 in *P. erythrogaster* (TS 174[1]), but to ventral portion of the anterior margin of neural arch 4 in other species of *Phoxinus* and in the outgroups (TS 174[0]). The neural spine bears a process at its posterior margin of the neural spine 4 in *P. phoxinus* (TS 175[0]) (Fig.80A); the process is absent in other species of *Phoxinus* and in the outgroups (TS 175[0]).

As in other ostariophysans (cf. Fink & Fink 1981), the anteriormost supraneural is absent in *Phoxinus*. Supraneural 3 (neural complex of Chen et al. 1984) is present at dorsal side of the neural arches 3 and 4, and posterior to neural arch 2. Supraneural 3 is a plate-like structure with constriction at the middle of its anterior and posterior margins. Its dorsal

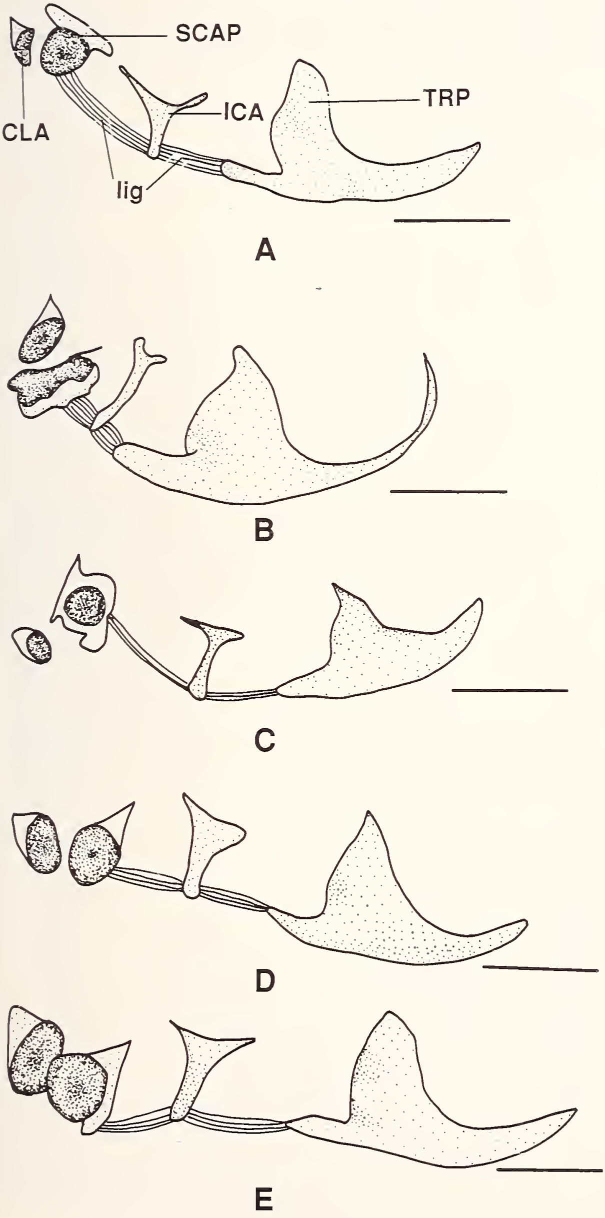

Fig.79: Lateral view of Weberian ossicles of *Phoxinus*. A: *P. oreas* (KU 3259, 55.0 mm SL); B: *P. neogaeus* (KU 8521, 53.0 mm SL); C: *P. eos* (KU 12255, 43.0 mm SL); D: *P. cumberlandensis* (KU 18934, 52.0 mm SL); E: *P. phoxinus* (CNUC uncat., 76.0 mm TL). Scale bars = 1 mm.

part (crest of neural complex – Cavender & Coburn 1992) is deeply grooved. It is narrow and relatively tall in *P. phoxinus, erythrogaster, brachyurus, neogaeus*, and in the outgroups (TS 176[0]); it is broad and relatively short in other species (TS 176[1]). In *P. phoxinus* and *eos*, the grooved portion of the supraneural is narrower (TS 177[1]) than that in other species of *Phoxinus* and in the outgroups (TS 177[0]). In *P. neogaeus*, the anterior portion of the dorsal margin of the supraneural is not grooved (TS 178[1]). In other species of *Phoxinus* and in the outgroups, its entire dorsal margin is grooved (TS 178[0])

The claustrum (Fig.77A-C, 79A-E) is located at the anterodorsal side of centrum 1. It covers the atrium sinus impar ventromedially, and the anterior portion of scaphium posteriorly. It is roughly triangular on lateral view, and no variation with phylogenetic significance was observed in *Phoxinus*.

The scaphium (Figs 77A-C, 79A-E) is located posteriorly to the claustrum. Coburn (1982) divided the scaphium into four parts: a cup at mesial, a posterodorsally directed spine, a ventromedial articulating process, and a blunt tubercle posteriorly off the lateral surface of the cup. Intraspecific variation is present in the morphology of different parts of the bone in *Phoxinus*. For instance, in some specimens of *P. phoxinus*, a notch is present on the margin of the cup; the notch is absent in other specimens of the same species; the posterodorsal spine is sharp in some specimens, it is blunt in other specimens of the same species.

The intercalarium (Figs 77A-C, 79A-E, 80B) is a roughly T-shaped bone and placed at the posterior to the scaphium anteriorly and anterior to the tripus. Via ligaments, the intercalarium connects with scaphium and tripus posteriorly. The intercalarium can be divided into three parts, a dorsolateral process, a dorsomedial process, and a main part. Generally, the dorsomedial process is shorter and blunter than the dorsolateral process. The dorsal margin of the bone is deeply concave in *P. neogaeus* and *oreas* (TS 179[1]); it is shallowly concave in other species of *Phoxinus* (TS 179[0]). The main part of the intercalarium is slender and relatively long in *P. erythrogaster* (TS 180[1]); it is broad and relatively short in other species of *Phoxinus* (TS 180[0]). The medial and lateral spines

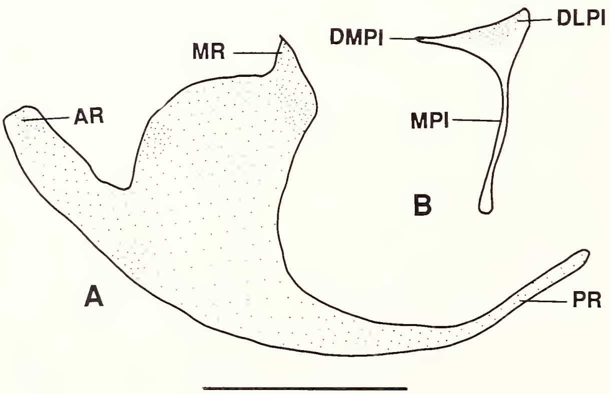

Fig.80: Lateral view of tripus (A) and intercalarium (B) of *Phoxinus erythrogaster* (KU 5773, 51.5 mm SL). Scale bar = 1 mm.

of the intercalarium are more slender in *P. oreas* (TS 181[1]) than in other species of the genus (TS 181[0]).

In the outgroups, the dorsal margin of the intercalarium is slightly concave, and all three parts of the bone are moderately broad.

The tripus (Figs.77A-C, 79A-E, 80A) is the largest element among the Weberian ossicle, and is located at the posterior portion of the bony chain formed by the ossicle. Three parts can be recognized for this triangular bone: anterior, medial, and posterior ramus. The anterior ramus extends and connects with ventral end of the intercalarium's main part via ligament. The medial ramus extends medially, and is connected with the lateral aspect of

Fig.81: Intermuscular bones of *Phoxinus tennesseensis* (UT 44,5274, 50.0 mm SL) (from caudal peduncle). Scale bar = 1 mm.

the centrum of the third vertebra. The posterior ramus is elongated and extends posteriorly and is concave. The posterior ramus is more slender and elongate in *P. neogaeus* and *erythrogaster* (TS 182[1]) than in other species of *Phoxinus* and in the outgroups (TS 182[0]).

Intermuscular bones. Intermuscular bones (myoseptal or intermyoseptal bones) (Fig.81) are placed in the myoseptum between two myotomes. In epaxial myotomes, the intermuscular bones are present from the first (or second) vertebral segment to the caudal fin base. In hypaxial myotomes, the bones exist from the posterior of the body cavity to the caudal fin base. Generally, intermuscular bones are thin and slender in shape, with or without a fork at the anterior end of the bones in epaxial myotomes or dorsal end of the bones in hypaxial myotomes. Some intermuscular bones are expanded at their posterior ends forming brush-like structures. No variations with phylogenetic significance are present among the species of *Phoxinus*.

Other supraneural bones (Figs.76A-D, 77A-C). Other supraneural bones are located median at the dorsal side of the body, from posterior of the supraneural bone 3 to the anterior of the origin of the dorsal fin in all *Phoxinus* species. The supraneural bones are plate-like, and roughly rectangular in shape.

Supraneural 4 is located between neural spine 5 and the supraneural 3. It is large and extends to the grooved portion of the supraneural 3 in *P. cumberlandensis* (TS 183[1]). It is small and extends to the dorsal of neural spine 4, but not to the grooved portion of supraneural 3 in all other species of the *Phoxinus* and in the outgroups (TS 183[0]). This supraneural bone is poorly developed, very small, and its anterior edge is far away from the posterior margin of neural spine 4 in *P. phoxinus*. In *P. erythrogaster*, supraneural 4 is pieced into two part, the anterior part is located on the dorsal to neural spine 4, and far away from neural spine 5; the posterior part is placed between neural spines 4 and 5 (TS 184[1]). This condition is absent in other species of *Phoxinus* or in the outgroups (TS 184[0]).

A single supraneural is present between two neighbor neural spines from neural spine 5 to the neural spine just anterior to the first dorsal pterygiophore. The supraneurals decrease in size posteriorly. The most posterior few supraneurals are very small. The last one just anterior to the first pterygiophore of the dorsal fin is absent in some specimens of *Phoxinus*.

Vertebrae

The vertebrae of species of *Phoxinus* can be divided into precaudal and caudal elements as defined below. Between the "normal" precaudal and caudal vertebrae two or three vertebrae are present as transitional elements (see below). The total number of the vertebrae, including numbers of the precaudal (the transitional elements included), and caudal elements, is given for each species in the species accounts. Number of vertebrae varies from 37 to 40, of which 18 to 20 are precaudal ones, and 17 to 21 are caudal ones.

Generally, the precaudal vertebrae, except the anterior four elements which were discussed in the "Weberian Apparatus", are almost monomorphic. Dorsally, each vertebra bears a neural arch and spine directed posterodorsally, a pair prezygopophyses, and a pair postzygopophyses. The prezygopophysis is located anteriorly to the neural arch, and decreases in size posteriorly, though the prezygopophysis on vertebra 5 is smaller than that on vertebra 6. The postzygopophysis is located at the posterior margin of the neural arch and articulates with the prezygopophysis of the next vertebra. The postzygopophysis is smaller than the prezygopophysis of the same vertebra; it is posteriorly directed, and slightly increasing in size posteriorly. The neural spines placed ventrally to the dorsal pterygiophores are shorter than those of the neural spines located anteriorly and posteriorly to the dorsal fin. Ribs ventrolaterally articulate with the parapophyses of the vertebrae.

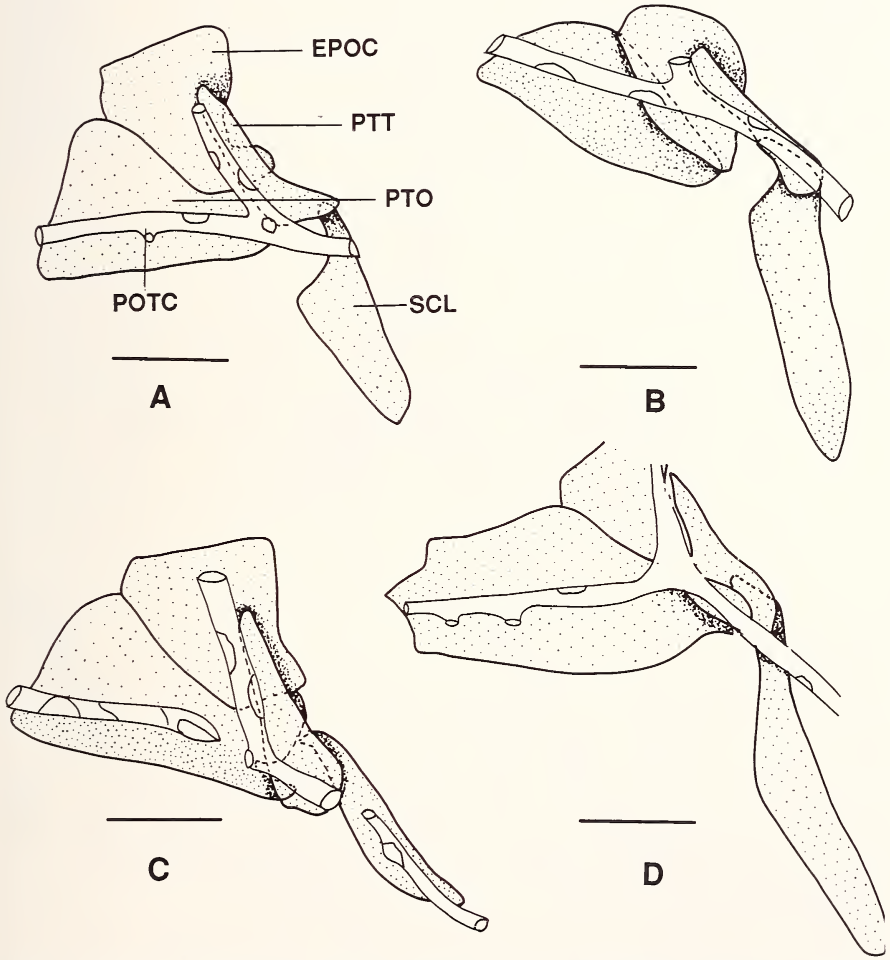

Fig.82: Dorsal view of pterotic, epioccipital, posttemporal, and supracleithrum of *Phoxinus*. A: *P. eos* (KU 12255, 43.0 mm SL); B: *P. phoxinus* (KU 22856, 58.0 mm SL); C: *P. cumberlandensis* (KU 18934, 52.0 mm SL); D: *P. oreas* (KU 3259, 52.2 mm SL). Scale bars = 1 mm.

Each caudal vertebra bears one neural arch and one neural spine, and paired prezygopophyses, postzygopophyses, haemal prezygopophyses, and haemal postzygopophyses. The prezygopophysis of the caudal vertebra is much smaller than that on precaudal vertebrae; however, the postzygophysis of the caudal vertebrae is larger than that of the precaudal vertebrae.

Each transitional vertebra bears an incomplete haemal arch without haemal spine, and two small free ribs.

No morphological variation with phylogenetic significance is observed in the vertebrae among the species of *Phoxinus*.

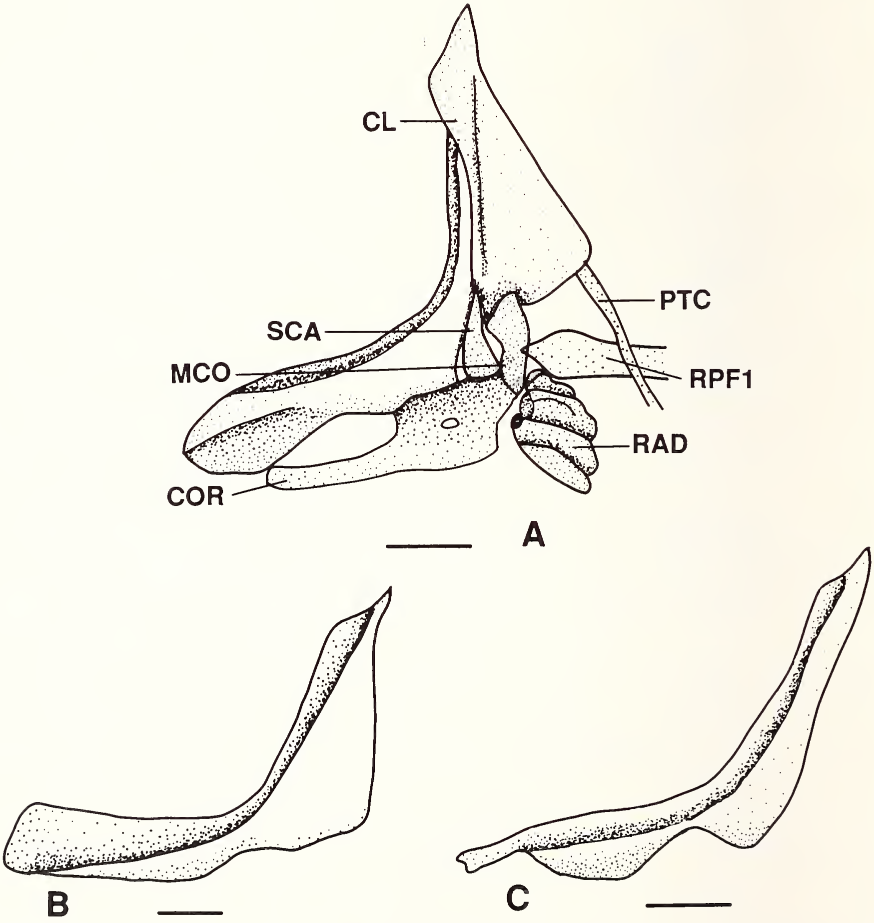

Fig.83: Lateral view of pectoral girdle (A), and cleithrum (B-C) of *Phoxinus*. A. *P. eos* (KU 12255, 43.0 mm SL), supracleithrum and posttemporal not shown; B: *P. phoxinus* (CNUC uncat., 76.0 mm TL); C: *P. issykkulensis* (P-10696, 42.4 mm SL). Scale bars = 1 mm.

Pectoral girdle and fin

In cyprinids, bones in the pectoral girdle include coracoid, mesocoracoid, scapula, posttemporal, supracleithrum, cleithrum, and postcleithrum. The coracoid, mesocoracoid, and scapula are endochondral bones and form the primary pectoral girdle; the remaining are dermal elements and form the secondary pectoral girdle.

Posttemporal (Fig.82A-D). The posttemporal is an elongated bone and located at the posterolateral side of the neurocranium. It overlaps the epioccipital dorsally and supracleithrum ventrally.

Generally, two conditions are present in shape of the posttemporal in *Phoxinus*. The posttemporal expands at its ventral portion in *P. erythrogaster, oreas, brachyurus*, and *cumberlandensis*, therefore the dorsal portion of the bone is narrower than the ventral one (TS 185[1]). The ventral portion does not expand in other species of *Phoxinus* and in the outgroups (TS 185[0]). The bone partially overlaps the dorsal side of the pterotic in *P. cumberlandensis, oreas, erythrogaster*, and *eos* (TS 186[1]). In *P. cumberlandensis*, more than half of the bone overlaps the pterotic; in *P. oreas* and *eos*, a small posterior portion of the

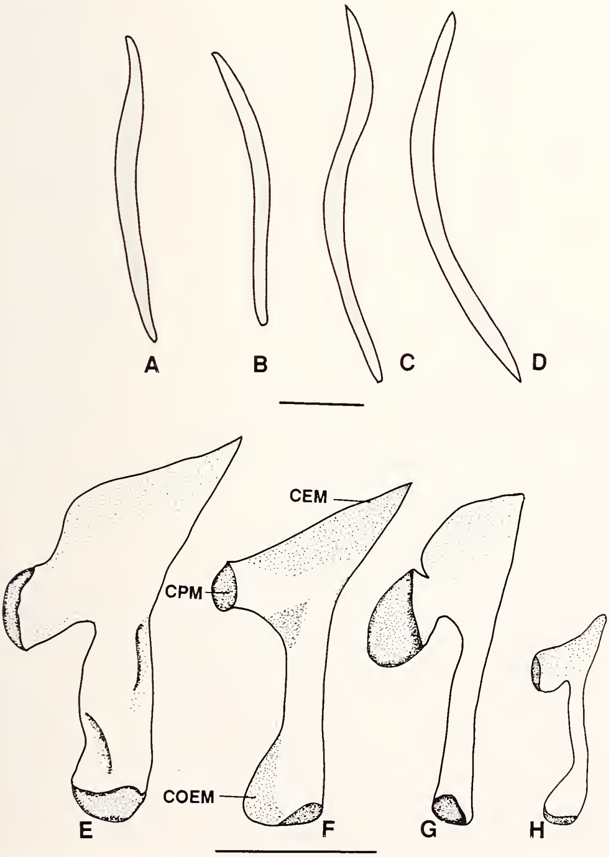

Fig.84: Anterior view of postcleithrum (A-D), and dorsal view of mesocoracoid (E-H) of *Phoxinus*. A: *P. cumberlandensis* (KU 18934, 552.0 mm SL); B: *P. eos* (KU 12255, SL 43.0 mm mm); C: *P. phoxinus* (CNUC uncat., 76.0 mm TL); D: *P. erythrogaster* (KU 5773, 52.0 mm SL); E: *P. erythrogaster* (KU 5773, 51.5 mm SL); F: *P. cumberlandensis* (KU 18934, 52.0 mm SL); G: *P. phoxinus* (CNUC uncat., 76.0 mm TL); H: *P. eos* (KU 12255, 33.0 mm SL). Scale bars = 1 mm.

posttemporal overlaps the pterotic; in *P. erythrogaster*, only a part of the anterior edge of the posttemporal overlaps the pterotic. The posttemporal does not overlap the pterotic in other species of *Phoxinus* or in the outgroups (TS 186[0]).

Supracleithrum (Fig.82A-D). The supracleithrum is an elongated, plate-like bone articulating with the posttemporal dorsomedially, and the cleithrum ventromedially. Its ventral part is slightly expanded. The dorsal portion of the bone is much narrower than its ventral portion in *P. eos* and *phoxinus* (TS 187[1]). The dorsal portion is only slightly narrower than the ventral portion in other species of *Phoxinus* and in the outgroups (TS 187[0]).

Cleithrum (Fig.83A-C). The L-shaped cleithrum is the largest element in the pectoral girdle. It articulates with supracleithrum dorsally, postcleithrum anteriorly, scapula, mesocoracoid, and coracoid posteriorly. Two parts can be recognized from the bone, the horizontal and ascending branches (process). The horizontal branch is the ventral part of the bone and roughly rectangular, with a large notch at the posterior margin. The ascending process is the dorsal part of the bone and roughly perpendicular to the horizontal branch. The ascending process is triangular, and its dorsal tip is sharp.

The notch of the horizontal branch forming the interosseus foramen with the coracoid at the posterior edge is deep in *P. issykkulensis* (TS 188[1]), but shallow in other species of *Phoxinus* and in the outgroups (TS 188[0]). The ventral margin of the ascending process is slightly sloped dorsally in *P. issykkulensis* (TS 189[1]); it is more sloped in other species of *Phoxinus* and in the outgroups (TS 189[0]).

Postcleithrum (Figs.83A, 84A-D). This is an elongated rod-like bone attaching to the mesial surface of the cleithrum's ascending process dorsally; its ventral end is sharp and free. No significant variation is present among the *Phoxinus* species.

Coracoid (Figs.83, 85A-F). The coracoid is a plate-like bone with expansion at the lateral part to form a broad part. It articulates with scapula laterally and with cleithrum posteriorly. The slender part, with the posterior margin of the cleithrum, forms the large interosseus foramen. In *P. cumberlandensis, eos, neogaeus*, and *erythrogaster*, the slender portion tapers medially; therefore, the posterior portion of the slender part is broader than the medial portion of the slender part in these species (TS 190[1]). In *P. phoxinus, brachyurus, issykkulensis, tennesseensis*, and *oreas*, the entire slender portion is almost equal in width, which is similar to that in the outgroups (TS 190[0]). In *P. cumberlandensis*, the bone bears a forked structure articulating with the scapula (TS 191[1]). The forked structure is absent in other species of *Phoxinus* and in the outgroups (TS 191[0]).

Mesocoracoid (Figs.84E-H). The mesocoracoid is a roughly T-shaped bone and articulates with the cleithrum posteriorly. For sake of description the following terms are given to different parts of the bone. The process articulating with the cleithrum is defined as cleithral process and its anterior end as the cleithral end. The end of the mesocoracoid articulating with coracoid as coracoidal end. The cleithral end is sharp in *P. erythrogaster, cumberlandensis* (TS 192[1]); blunt in other species of *Phoxinus* and in the outgroups (TS 192[0]). The cleithral process is straight in *P. cumberlandensis* (TS 193[1]); it is slightly bent in other species of *Phoxinus* and in the outgroups (TS 193[0]). Moreover, a notch is present at the medial margin of the cleithral process in *P. phoxinus* (TS 194[1]); this notch

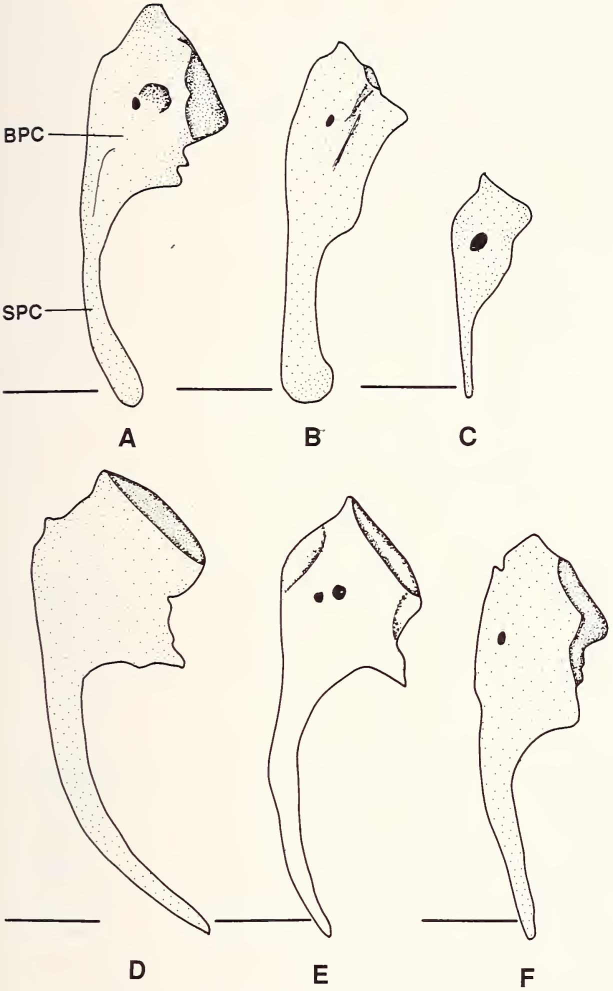

Fig.85: Dorsal view of coracoid of *Phoxinus*. A: *P. oreas* (KU 3259, 55.0 mm SL); B: *P. phoxinus* (CNUC uncat., 76.0 mm TL); C: *P. eos* (KU 12255, 33.0 mm SL); D: *P. neogaeus* (KU 8521, 53.0 mm SL); E: *P. erythrogaster* (KU 5773, 51.5 mm SL); F: *P. cumberlandensis* (KU 18934, 52.0 mm SL). Scale bars = 1 mm.

is absent in other species of *Phoxinus* and in the outgroups (TS 194[0]). The coracoidal end expands in *P. cumberlandensis* and *eos* (TS 195[1]); whereas it does not expand in other species of *Phoxinus* or in the outgroups (TS 195[0]).

Scapula (Fig.83A). The scapula bears a large round foramen at its central, and different facets articulating the cleithrum, mosocoracoid, coracoid, and first pectoral fin-ray. No significant variation is present among the species of *Phoxinus*.

Radials (Figs.83A, 86, 87A-F). Four radials are present in each pectoral fin in *Phoxinus*, namely the radials 1, 2, 3, and 4 (Figs.83A, 87A-F).

The first radial is the shortest among the four. Two articular facets are present at the la-

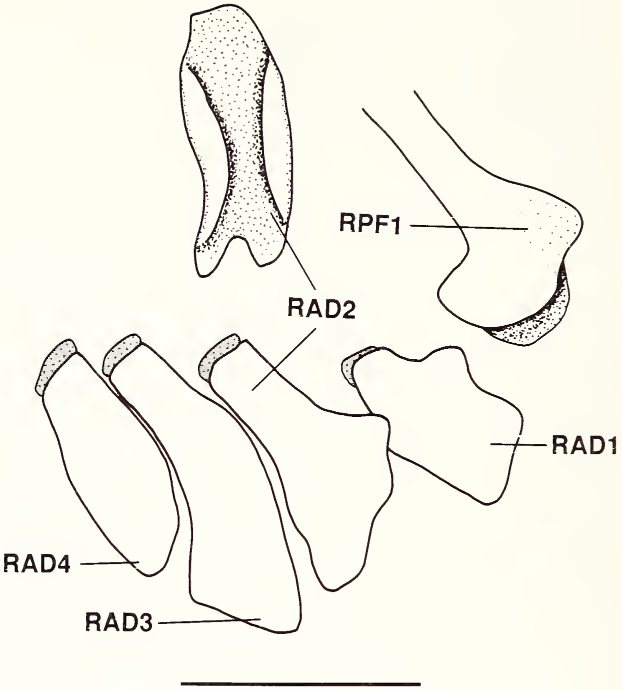

Fig.86: Dorsal view of pectoral radials of *Phoxinus phoxinus* (CNUC uncat., 76.0 mm TL). Scale bars = 1 mm.

teral side of the bone. The two facets articulate with the first pectoral ray and are far away from one another. In *P. eos*, the medial facet is very high and forms a process (TS 196[1]). The facet is much lower in other species of *Phoxinus* and in the outgroups (TS 196[0]).

Radial 2 (Figs.86, 87A-F) bears a trough at its lateral side to articulate with the medial side of radial 1. The bone is triangular in *P. cumberlandensis, erythrogaster, phoxinus*, and *oreas* (TS 197[1]); it is narrow and slender in other species of *Phoxinus* and in the outgroups (TS 197[0]). A process is present at the medial margin of radial 2 in *P. eos* (TS 198[1]); the process is absent in other species of *Phoxinus* and in the outgroups (TS 198[0]).

Radial 3 (Figs.86, 87A-F) is an elongate bone bearing a trough at the lateral side articulating with the medial of radial 2. A process is present at its anteromedial side in *P. cumberlandensis* (TS 199[1]); the process is absent in other species and in the outgroups (TS 199[0]).

Radial 4 (Figs.86, 87A-F) is an elongated bone and does not bear variation with phylogenetic significance in *Phoxinus*.

In *Phoxinus*, 13 to 18 pectoral fin-rays are present with intraspecific variation. See Species Accounts for discussion on variation in the numbers of the pectoral rays for each species. The pectoral rays increase in number with age (Hill & Jenssen 1968). All rays, except the first one, do not bear variation with phylogenetic significance in *Phoxinus*.

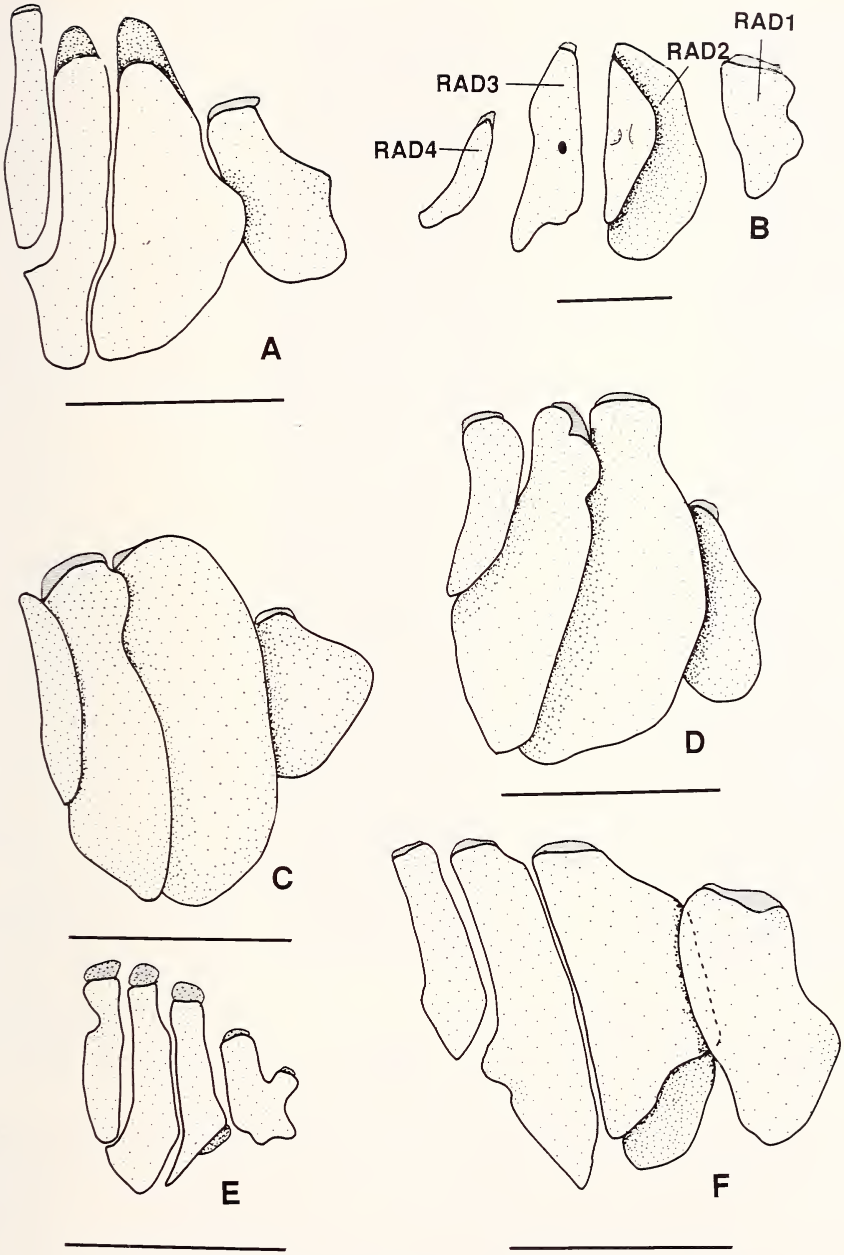

Fig.87: Dorsal view of pectoral radials of *Phoxinus*. A: *P. cumberlandensis* (KU 18934, 52.0 mm SL); B: *P. neogaeus* (KU 8521, 53.0 mm SL); C: *P. erythrogaster* (KU 5773, 51.5 mm SL); D: *P. issykkulensis* (P-10696, 42.4 mm SL); E: *P. eos* (KU 12255, 33.0 mm SL); F: *P. oreas* (KU 3259, 55.0 mm SL). Scale bars = 1 mm.

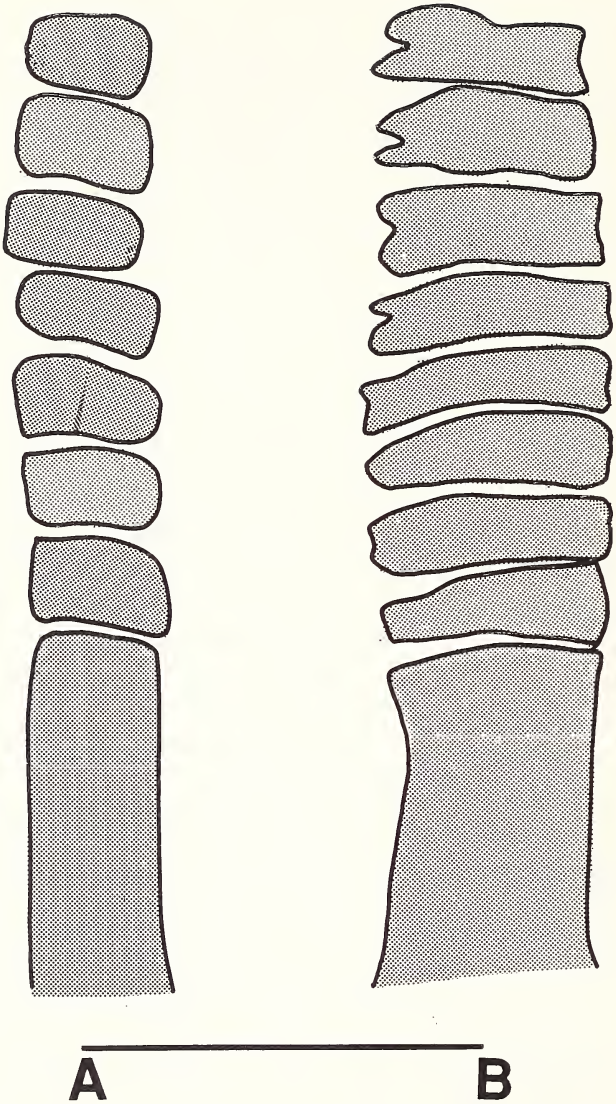

Fig.88: Dorsal view of a portion of the larger hemitrichia of the first pectoral fin ray of breeding males of (A) *Phoxinus erythrogaster* (KU 5773, 51.5 mm SL), and (B) *P. neogaeus* (KU 8521, 53.0 mm SL). Scale bars = 1 mm.

The first pectoral ray is the longest, thickest and strongest in all of the pectoral rays. The two hemitrichia can be easily separated from one another, one is smaller than the other. The base of the larger one is forked and articulates with the scapula; the medial side of the bone is concave and contacts with the smaller one. Variation of the ray is present in its segmentation in breeding males (Fig.88A-B). In breeding male of *P. neogaeus*, the segments are broad and short, most of the segments bear a notch at its lateral margin (TS 200[1]). In other species and in the outgroup, the segments are narrow and relatively high without any notch at the lateral margin (TS 200[0]).

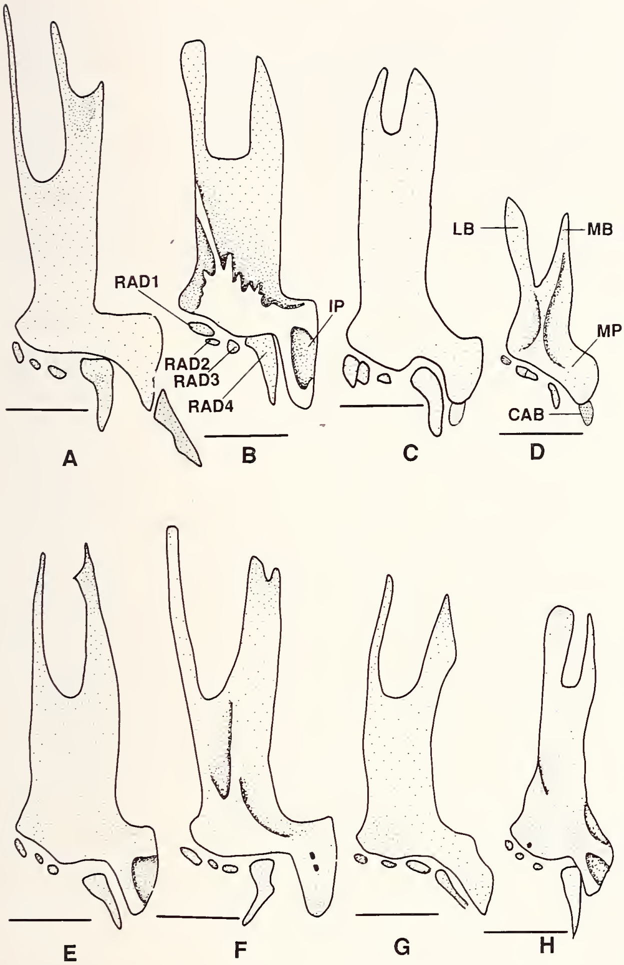

Fig.89: Dorsal view of pelvic girdle of *Phoxinus*. A: *P. phoxinus* (CNUC uncat., 76.0 mm TL); B: *P. erythrogaster* (KU 5773, 51.5 mm SL); C: *P. neogaeus* (KU 8521, 53.0 mm SL); D: *P. issykkulensis* (P-10696, 42.4 mm SL); E: *P. cumberlandensis* (KU 18934, 52.0 mm SL); F: *P. oreas* (KU 3259, 55.0 mm SL); G: *P. tennesseensis* (UT 44.5274, SL 50.0 mm SL); H: *P. eos* (KU 12255, 43.0 mm SL). Scale bars = 1 mm.

Pelvic girdle and fin

The pelvic girdle (Fig.89A-H) is composed of a single, expanded basipterygium. Anteriorly, it is forked, thus two pelvic plates, the medial and lateral plate, are formed. Posterior portion of the basipterygium forms a medial process which bears a posterior ischiac project. One elongated triangular radial and three small ones articulate with the posterior margin of the basipterygium.

Variation is present in the general shape of the basipterygium. In *P. phoxinus, oreas, issykkulensis*, and *cumberlandensis*, the anterior fork is deep (depth of the fork is equal or longer than the length of the unforked part of the bone, the length of the ischiac project not included) (TS 201[0]); the fork is shallow (depth of the fork is much less than the length of the unforked part of the bone) in other species of *Phoxinus* (TS 201[1]). The medial pelvic plate is broad and forked in *P. oreas* and *phoxinus* (TS 202[0]); it is narrow and unforked in other species of *Phoxinus* (TS 202[1]). The ischiac process is broad, short triangular in *P. neogaeus, issykkulensis, cumberlandensis*, and *eos* (TS 203[1]); the process is an elongated triangle in other species of *Phoxinus* (TS 203[0]).

In the outgroups, the anterior fork is deep, the medial branch is broad and forked, and the ischiac process is narrow and elongated triangular-shaped.

A cartilage (Fig.89A, D) exists at the posterior to the ischiac process in *P. issykkulensis, neogaeus*, and *phoxinus* (TS 204[1]). The cartilage is small and short rod-like in *P. issykkulensis* and *neogaeus*; whereas it is an elongated triangle in *P. phoxinus*. This cartilage is absent in other species and in the outgroups (TS 204[0]).

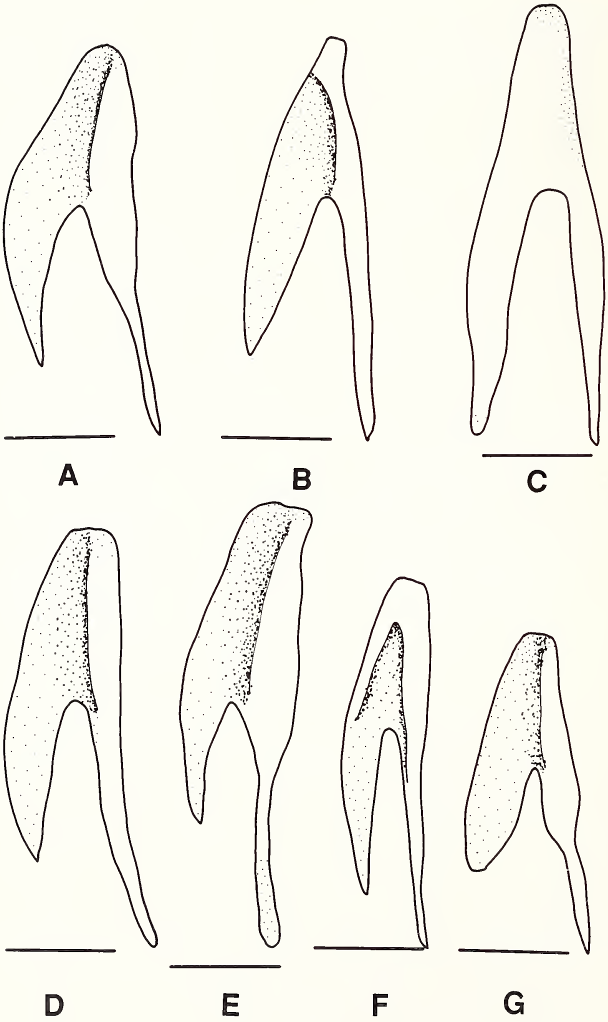

Fig.90: Lateral view of proximal part of the first dorsal pterygiophore of *Phoxinus*. A: *P. cumberlandensis* (KU 18934, 52.0 mm SL); B: *P. neogaeus* (KU 8521, 53.0 mm SL); C: *P. brachyurus* (MCZ 3006, 75.9 mm SL); D: *P. oreas* (KU 3259, 52.2 mm SL); E: *P. phoxinus* (CNUC uncat., 76.0 mm TL); F: *P. tennesseensis* (UT 44.5274, 50.0 mm SL); G: *P. eos* (KU 12255, 43.0 mm SL). Scale bars = 1 mm.

Four radials are present at the posterior margin of the basipterygium. The radials articulate with the basipterygium anteriorly, and the anterior end of the pelvic rays posteriorly. Radials 1 to 3 (from distal to proximal) are small, cubic, or spherical in shape. Significant variation is absent in these bones in *Phoxinus*. Radial 4 is the largest among the four radials. Radial 4 is an elongated triangle in *P. cumberlandensis, erythrogaster, eos, phoxinus, neogaeus, oreas*, and in the outgroups (TS 205[0]); it is an elongated bar in other species of *Phoxinus* (TS 205[1]).

Seven to eight rays of the pelvic fin are generally present in *Phoxinus*. See below for discussion on variation of the number of fin-rays for each species of *Phoxinus*.

Dorsal Fin

Eight pterygiophores are present in all *Phoxinus* species. In cyprinids, each pterygiophore is composed of three portions: proximal, middle, and distal parts (Harder 1975, Chen 1987a). The proximal part (Fig.90A-G) is elongated and is the main element of pterygiophore. The middle part is short bar-shaped; its dorsal and ventral sides are concave to articulate with the distal and proximal parts of the pterygiophore respectively. The distal part is a small spherical bone. The middle and distal parts in all pterygiophores are similar to one another in shape and without variation among the species of *Phoxinus*. The proximal parts of the second to the eighth pterygiophores are not forked and similar to one another in shape, but decrease in size posteriorly. The proximal part of the first pterygiophore, the largest one, is forked at its ventral portion, and expanded at its middle portion. The proximal part of the first pterygiophore in *P. tennesseensis* is slender (TS 206[1]) than that in other species of *Phoxinus* or in the outgroups (TS 206[0]). In *P. brachyurus*, the fork on the proximal part of the first pterygiophores is deep, the anterior process of the fork is almost equal to the posterior process in length (TS 207[1]). In other species

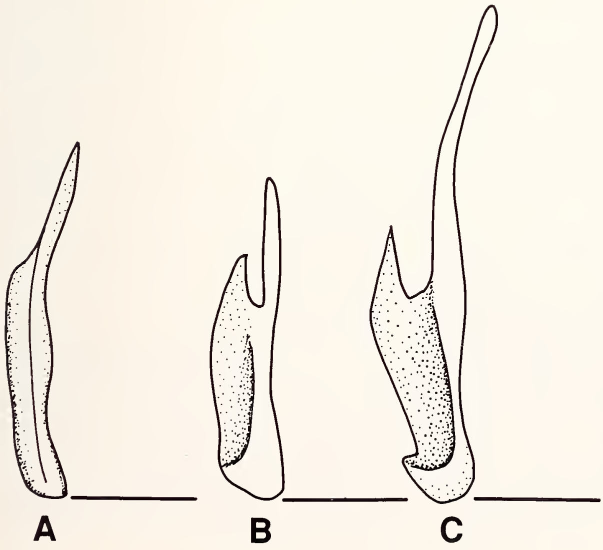

Fig.91: Lateral view of the proximal part of the first pterygiophore of anal fin of *Phoxinus*. A: *P. eos* (KU 12255, 43.0 mm SL); B: *P. tennesseensis* (UT 44.5274, 50.0 mm SL); C: *P. oreas* (KU 3259, 52.2 mm SL). Scale bars = 1 mm.

of *Phoxinus* and in the outgroups, the anterior branch is much shorter than the posterior one (TS 207[0]).

One to three procurrent rays, and seven to eight dorsal rays are present in the species of *Phoxinus*. Intraspecific variation of the number of rays is present in the genus; see "Species Account" for discussion on the variation of fin rays for each species.

Anal fin

Eight pterygiophores of the anal fin are present in all *Phoxinus* species; they are similar in shape to dorsal pterygiophores. Each pterygiophore consists of proximal, medial and distal parts. The second to the eighth pterygiophores are similar to each other (though the size decreases posteriorly), not forked, without variation among species of *Phoxinus*. However, the proximal part of the first pterygiophore is forked in *P. oreas* and *P. tennesseensis* (TS 208[1]; Fig.91B-C); it is unforked in other species of *Phoxinus* and in the outgroups (TS 208[0]; Fig.91A).

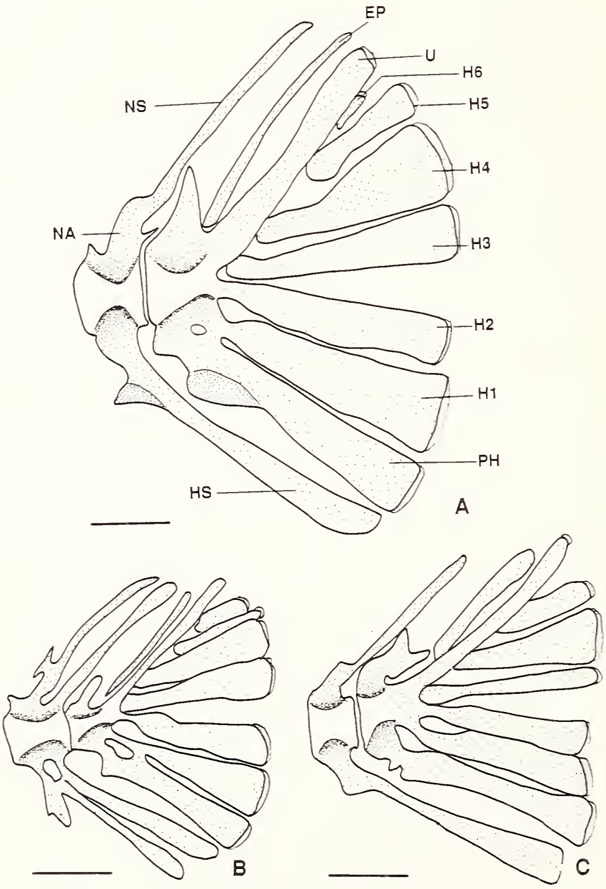

Fig.92: Lateral view of caudal skeleton of *Phoxinus*. A: *P. brachyurus* (MCZ 3006, 75.9 mm SL); B: *P. phoxinus* (KU 22856, 58.0 mm SL); C: *P. cumberlandensis* (KU 18934, 52.0 mm SL). Scale bars = 1 mm.

Similar to the dorsal fin-ray, one or two procurrent rays and seven or eight anal fin-rays are present in the species of *Phoxinus*. Intraspecific variation of the number of rays is present; see "Species Account" for discussion on the variation for each species.

Caudal skeleton and fin rays

The general morphology of the caudal skeleton of *Phoxinus* (Fig.92A-C) is similar to that of other cyprinids (c.f. Fink & Fink 1981, Buhan 1972, Mayden 1989). Variation of the caudal skeleton in *Phoxinus* is found in the single epural and hypural 6. The epural is more slender and longer in *P. brachyurus* and *P. erythrogaster* (TS 209[1]) than that in other species of the genus and in the outgroups (TS 209[0]). Hypural 6 is absent in *P. cumberlandensis* and *P. oreas* (TS 210[1]); it is present in other species of the genus or in the outgroups (TS 210[0]).

Two types of caudal rays can be recognized, the principal and procurrent rays. Similar to other cyprinids (c.f. Fink & Fink 1981, Schultze & Arratia 1989), principal caudal fin rays in *Phoxinus* are 19 (10+9). The dorsal procurrent rays are from four to 12 in number, ventral procurrent rays from four to 10, both of which bear intraspecific variations (see "Species Account").

PHYLOGENETIC RELATIONSHIPS OF THE SPECIES OF *PHOXINUS*

Phylogenetic Relationships

Appendix II shows distribution of the polarities of the 210 transformation series among the nine species of *Phoxinus*. Based on the data matrix in Appendix II, PAUP 3.0 (with exhaustive search) generated 2,027,025 trees from 398 steps to 493 steps in tree length. The most parsimonious tree produced by PAUP is shown in Figure 93, with tree length = 398 steps, CI = 0.546 (CI excluding uninformative transformation series = 0.436), HI = 0.454 (HI excluding uninformative transformation series = 0.564).

Two major clades are included in the genus *Phoxinus*, i.e., *brachyurus*-clade, and *erythrogaster*-clade. The *brachyurus*-clade consists of three recognized Eurasian species of the genus and one North American species, *P. neogaeus*. The *erythrogaster*-clade includes the other five North American species of the genus, without *P. neogaeus*.

The synapomorphies for each node (Fig.93) are listed below. The apomorphies of each species are also listed under the appropriate node.

Node A. This node unites the nine species of *Phoxinus* as a monophyletic group. Eight synapomorphies support the monophyly of *Phoxinus*: supraorbital canal interrupted between nasal and frontal bones; preopercular canal ending at the middle of the ascending arm of preopercle; preoperculomandibular canal interrupted into mandibular and preopercular canals; breast scales deeply embedded in breeding males; breast scale bearing a series of tubercles at its apical margin in breeding males; scale on caudal peduncle bearing three or more tubercles at its apical margin in breeding males; orbital septum lower; pharyngeal pad of occipital bone bearing an anterior process.

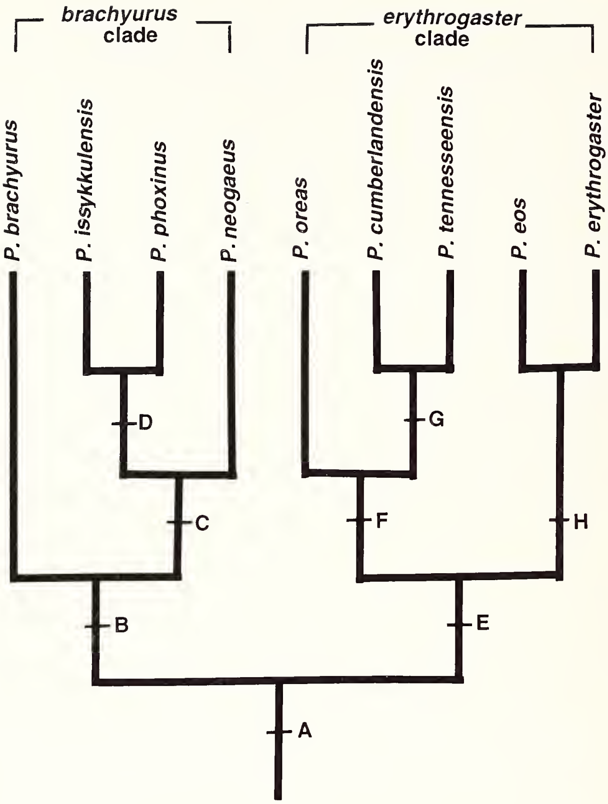

Fig.93: Phylogenetic hypothesis of relationships among species of *Phoxinus* (tree length =398, CI = 0.546, HI = 0.454). See text for the synapomorphies supporting each node.

Node B. This node groups four species of *Phoxinus* as the *brachyurus*-clade, including *P. brachyurus, issykkulensis, neogaeus*, and *phoxinus*. Nineteen synapomorphies are shared by these species: 1[1], 3[1], 25[1], 46[1], 52[1]* (autapomorphy), 59, 69, 75, 88*[1], 90*[1], 106[1], 107[1], 109[1], 110[1], 114[1], 116[1]*, 150[1], 173[1], and 186[1].

P. brachyurus is the sistergroup of the *Phoxinus* species complex, and bears the following 26 apomorphies: 23[1], 28[1], 30[1], 33[1], 37[1], 45[1], 49[1], 57[1], 61[1], 71[1], 73[1], 77[1], 82[1], 94[1], 103[1], 104[1], 108[1], 126[1], 131[1], 141[1], 153[1], 185[1], 201[1], 205[1], 207[1], and 209[1].

Node C. Species united at Node C are *P. issykkulensis, neogaeus*, and *phoxinus*, which form the *phoxinus* species complex. These three species share the following 10 synapomorphies: 41[1], 78[1]*, 79[1]*, 89[1]*, 97[1], 112[1], 118*[1], 124[1], 139[1], and 204[1]*.

P. neogaeus is the sistergroup of the *phoxinus* species pair (*P. phoxinus* + *issykkulensis*) and bears the following 34 apomorphies: 2[1]*, 7[2], 8[1], 26[1], 32[1], 34[1], 38[1], 40[1], 42[1], 43[1]*, 48[1], 54[1], 68[1], 74[1]*, 94[1], 96[1], 102[1], 104[1], 113[1], 120*[1], 132[1], 134[1], 140[1], 151[1], 152[1], 158[1], 161[1], 178[1]*, 179[1], 182[1], 190[1], 200[1], 201[1], and 203[1].

Node D. This node identifies *P. phoxinus* and *issykkulensis* as the *phoxinus* species pair. These two species share the following 13 synapomorphies: 35[1], 66[1], 67[1], 73[1], 100 [0] (reversal), 122[1], 125[1], 127[1], 131[1], 133[1], 144[1], 145[1], and 154[1]*.

P. phoxinus bears the 59 following apomorphies: 5[1], 6[1], 9[1], 10[1], 11[1], 12[1], 14[1], 16[1], 17[1], 18[1], 19[1], 20[1], 21[1], 22 [2], 24[1], 25[1], 30[1], 31[1], 32[1], 38[1], 46[1], 47[1], 48[1], 54[1], 55[1], 57[1], 60[1], 62[1], 64[1], 69[1], 83[1], 85[1], 87[1], 95[1], 102[1], 105[1], 107[1], 123[1], 126[1], 128[1], 140[1], 141[1], 146[1], 148[1], 149[1], 151[1], 152[1], 157[1], 161[1], 165[1], 168[1], 172[1], 175[1], 177[1], 187[1], 189[1], 194[1], 197[1], and 202[1].

P. issykkulensis bears the following 25 apomorphies: 3[1], 8[1], 28[1], 31[1], 33[1], 36[1], 42[1], 44[1], 49[1], 59[1], 98[1], 101[1], 103[1], 109[1], 110[1], 113[1], 115[1], 132[1], 142[1], 156[1], 158[1], 176[1], 188[1], 203[1], and 205[1].

Node E. This node groups the five North American species of *Phoxinus* as the *erythrogaster*-clade, including *P. cumberlandensis, tennesseensis, oreas, eos*, and *erythrogaster*. The following nine synapomorphies are shared by these five species: 29[1]*, 34[1], 40[1], 67[1], 132[1], 134[1], 141[1], 143[1]*, and 164[2]*.

Node F. *P. oreas, cumberlandensis*, and *tennesseensis* are united at this node as the *oreas* species complex, the sistergroup of the *erythrogaster* species pair (*P. erythrogaster* + *eos*). The following 13 synapomorphies are shared by the *oreas* species complex: 24[1]*, 32[1], 35[1], 49[1], 66[1], 69[1], 93*[1], 96[1], 111[1], 112[1], 113[1], 140[1], and 176[1].

P. oreas is the sistergroup of the two species *P. cumberlandensis* and *tennesseensis*, and bears the following 26 apomorphies: 22[1], 23[1], 28[1], 29[3]*, 53[1], 57[1], 59[1], 65[1], 70[1], 97[1], 101[1], 102[1], 130[1], 139[1], 144[1], 145[1], 146[1], 150[1], 159[1], 179[1], 181[1]*, 185[1], 197[1], 202[1], 208[1], and 210[1].

Node G. *P. cumberlandensis* and *tennesseensis* are grouped at this node. These two species share the following 11 synapomorphies: 8[1], 27[1], 41[1], 42[1], 51[1]*, 86[1], 117[1], 122[1], 125[1], 165[1], and 173[1].

P. cumberlandensis is the sistergroup of *P. tennesseensis*, and bears the following 44 apomorphies: 1[1], 7[1], 15[1]*, 28[1], 29[2]*, 36[1], 40[0] (reversal), 45[1], 46[1], 50[0] (reversal), 54[1], 56[1]*, 63[1]*, 65[1], 68[1], 69[1], 72[1]*, 75[1], 76[1]*, 80[1], 81[1]*, 91[1]*, 121[1]*, 126[1], 127[1], 129[1], 133[1], 135[1], 137[1], 138[1]*, 160[1]*, 166[1]*, 170[1], 183[1], 185[1], 190[1], 191[1]*, 192[1], 193[1]*, 195[1], 197[1], 199[1], 203[1], and 210[1].

P. tennesseensis bears the following 20 apomorphies: 9[1], 22[1], 25[1], 33[1], 53[1], 57[1], 58*[1], 67[0] (reversal), 71[1], 102[1], 104[1], 106[0] (reversal), 130[1], 141[1], 159[1], 186[1], 201[1], 205[1], 206[1]*, and 208[1].

Node H. *P. eos* and *erythrogaster* are grouped at this node as the *erythrogaster* species pair and share the following 17 synapomorphies: 1[1], 22[1], 42[1], 64[1], 86[1], 97[1], 99[1]*, 104[1], 123[1], 131[1], 137[1], 139[1], 161[1], 163[1]*, 171[1], 190[1], and 201[1].

P. eos bears the following 17 apomorphies: 1[1], 22[1], 42[1], 64[1], 86[1], 97[1], 99[1], 104[1], 123[1], 131[1], 137[1], 139[1], 161[1], 163[1], 171[1], 190[1], and 201[1].

P. erythrogaster bears the following 35 apomorphies: 4[1], 5[1], 13[1], 32[1], 35[1], 36[1], 39[1], 49[1], 50[1], 65[1], 70[1], 84[1], 92[1], 108[1], 111[1], 114[1], 124[1], 125[1], 133[1], 135[1], 145[1], 146[1], 150[1], 153[1], 155[1], 165[1], 167[1], 174[1], 180[1], 182[1], 184[1], 185[1], 192[1], 197[1], and 209[1].

Discussion on the phylogenetic relationships of the species of *Phoxinus*

The phylogenetic relationships within *Phoxinus* proposed herein indicate two clades in the genus, the *brachyurus*-clade including all three Eurasian species and *P. neogaeus*, and the *erythrogaster*-clade consisting of the other five North American species (Fig.93). This result supports, in general, the phylogenetic hypotheses among some *Phoxinus* species proposed by Joswiak (1980) based on allozyme data, and Starnes & Starnes (1978) and Starnes & Jenkins (1988) based on external and osteological morphology. However, I disagree with Joswiak's (1980) placement of *Phoxinus* species into three subgenera: *Phoxinus* (including *P. phoxinus*), *Pfrille* (consisting of *P. neogaeus*), and *Chrosomus* (including all other North American species of the genus). If Joswiak's (1980) proposal is followed, the subgenus *Phoxinus* would include all species of the *brachyurus* clade, except *P. neogaeus*, or the subgenus *Pfrille* would consist of all species of the *brachyurus* clade excluding *P. phoxinus*. Either way results in the subgenera *Phoxinus* and *Pfrille* being paraphyletic, which is logically inconsistent with the phylogenetic tree, and not acceptable in the phylogenetic study (Hennig 1966, Wiley 1981, Wiley et al. 1991).

The close relationship between *P. phoxinus* and *P. neogaeus* (both are in the *phoxinus* species complex) has been accepted since the description of *P. neogaeus* was published by Cope (1869), although some authors assigned *P. neogaeus* to another genus (*Pfrille*). However, the close relationship has never been critically reviewed. The characters thought to support this relationship are either plesiomorphic, such as two rows of pharyngeal teeth, short intestine (e.g., Gasowska 1980), or occur in all *Phoxinus* species, such as tuberculation on breast scales in breeding males (e.g., Hubbs & Brown 1929, Gasowska 1979). Ten synapomorphies found in this study support strongly the close relationship between *P. neogaeus* and *P. phoxinus* plus *issykkulensis*.

Mahy (1975c) proposed *P. erythrogaster, oreas*, and *eos* as three subspecies of a single species *P. erythrogaster*, and *erythrogaster* as the ancestor of *P. oreas* and *P. eos*. My study does not support Mahy's hypothesis and shows the three "subspecies" as different species. Fig.93 indicates that it is hardly to propose *P. erythrogaster* be the ancestor of *P. eos* and *oreas*. Data from allozymes (Joswiak 1980) also support my phylogenetic hypothesis, not the one of Mahy (1975c). Mahy's failure to recognize the difference of these three species might be "due to his choice of characters" (personal communication of Starnes to Joswiak, cited from Joswiak 1980).

Gasowska (1979) placed *P. neogaeus* in a subgenus *Pfrille* of genus *Phoxinus*, and the other three North American species (*P. eos, oreas*, and *erythrogaster*) into two different genera: *P. eos* and *P. erythrogaster* in *Chrosomus*, and *oreas* in a new genus *Parchrosomus*. Gasowska (1979) correctly recognized the close relationship between *P. neogaeus* and *P. phoxinus* based on the breast tuberculation (though it is a plesiomorphic character in the genus of *Phoxinus*). However, she seemed not to recognize that similar breast scale tuberculation occurs in other North American *Phoxinus* species. If *P. oreas* was considered as a separate genus from *Phoxinus*, the other species of *Phoxinus* would form a paraphyletic group.

Biogeography of *Phoxinus*

Among North American freshwater fishes, the two largest families, Cyprinidae and Percidae, comprise the major part of the primary and secondary Recent freshwater fish community (Patterson 1981, Mayden 1991). These two families are considered by some to have originated in Europe and/or Asia (Banarescu 1972, 1989). Three hypotheses have been proposed to interpret the relationship between the freshwater fish faunae of Eurasia and North America, i.e., "Amphi-Atlantic" hypothesis, "Old Pacific connection" vicariant hypothesis, and "Bering land connection" dispersal hypothesis. These hypotheses can be summarized as following.

1) The Amphi-Atlantic hypothesis implies that the freshwater fish fauna in Europe and in North America bears a closer relationship than either does to the fauna in Asia (see Banarescu & Coad 1991). The trans-Atlantic connection between Europe and North America was present until Early Eocene (Brown & Gibson 1983; Briggs 1986). Patterson (1981) claimed that relationships of *Amia* species indicated North America more closely related to Europe than to Asia. Wiley (1992) proposed that the ancestor of Percidae probably originated in Early Tertiary before the final opening of the North Atlantic, without indicating the place of the ancestral origin. Banarescu (1989) stated that the ancestor of the Percini of Percidae, prevailing in Europe, and the Etheostomatini, endemic to North America, was split by the breaking down of the Atlantic connection between North America and Europe. The above hypotheses might be considered to support an "Amphi-Atlantic" hypothesis. No evidence from Cyprinidae was found supporting this hypothesis because no cyprinid was known from Europe before the Oligocene (Kimmel 1975, Cavender 1986, 1991, Bogutskaya 1991), and no cyprinid fossils have been found in North America until the Oligocene (Cavender 1986, 1991). The Atlantic connection seems too early for the migration (if there was a migration) of the ancestor of cyprinids into North America from Europe, or vice versa.

2) The Old Pacific Connection hypothesis claims that east Asia and North America share a close relationship (see Howes 1984), and the splitting of the ancestor of (at least some) cyprinids in North America and Asia was due to the separation between Asia and North America. A series of collisions among several plates between Siberia and North America happened during the Cretaceous (Fujita 1978). This hypothesis might be supported by the distribution of Polydontidae (Patterson 1981, Grande & Bemis 1991), and the relationships of some insect groups (e.g., caddisflies; see Ross 1974). It may explain the distribution of the monotypic genus *Notemigonus* of eastern North America and its relationship to the genus *Alburnoides* of southwest Asia (Banarescu & Coad 1991). It may also be relevant to the relationship within the aspinine of cyprinids (Howes 1984). However, the earliest cyprinid was found in the Oligocene in North America (Cavender 1986, 1991) which is much younger than the Cretaceous.

3) The "Bering Land Connection" dispersal hypothesis relies on exposure above see level of Bering land connection between Asia and North America. A Bering land connection existed through most of the Tertiary, and was present again during the Pleistocene (Hopkins 1967, Joswiak 1980, Briggs 1986). "Relatively brief inundations apparently took place in the Late Miocene and Late Pliocene during the interglacial stages" (Briggs 1986:7). The "Bering land connection" dispersal hypothesis implies that the ancestor of the North American cyprinids originated in east Asia, and dispersed into North America from Asia through the Bering land connection (Briggs 1979, 1986, Joswiak 1980). Banarescu (1989) proposed that the ancestor of some North America percids (*Perca*) originated in Europe migrated into Asia and then into North America through the Bering land connection. The "Bering land connection" dispersal hypothesis is accepted by some authors to explain the relationships of (at least) the cyprinid fauna in Asia and North America (e.g., Briggs 1979, Banarescu 1989).

The Bering land connection played an important role in the formation of the North American freshwater fish fauna because the connection provided a possible way for the exchange of the freshwater fishes between North America and Asia, and provided some vicariants for the speciation of the ancestors of (at least) some freshwater fishes on the two continents after the submission of the Bering land connection. As discussed below, I propose the Bering land connection be important for the speciation of *Phoxinus* as well. My interpretation of the role of the connection, however, is based on view of the vicariance biogeography (Wiley 1988), i.e., I propose a "Bering land connection" vicariant hypothesis to interpret the biogeography of *Phoxinus*.

The area cladogram based on the phylogenetic relationship of *Phoxinus* indicates a close relationship between Asia, Europe and North America (Fig.94). However, in order to correctly understand the area cladogram (Fig.94), it is necessary to discuss the geographic distribution of *P. phoxinus*. *P. phoxinus* occurs widely in Europe (whole Europe except southern Spain and Iceland – Sterba 1989), and in central and eastern Asia. The populations of the species in Europe might be interpreted as immigrant from Asia because the European cyprinids had an Asian origin (Banarescu 1960). The east Asian population of *P. phoxinus* was also considered an immigrant by some (Banarescu & Coad 1991). Therefore, *P. phoxinus* might have originated in central Asia, and then dispersed into Europe and East Asia. Thus what the area cladogram (Fig.94) really indicates is that North America bears a closer relationship with Central Asia than with either Europe or East Asia. This implies that the ancestor of the genus *Phoxinus* occurred in North America and Central Asia (not East Asia), and was split by separation of Asia and North America into the ancestor of the *brachyurus* clade in Asia, and the ancestor of the *erythrogaster* clade in North America (cf. Figs.93, 94). This ancestor might have occurred in North America and Asia during (or before) the Miocene when the Bering land connection existed, and was split by submission of the Bering land connection in the Tertiary. Because no fossils of species of *Phoxinus* are known, I am not able to identify the age of the origin for the genus using the fossil record. However, based on the alloelectrophoretic studies on *Phoxinus* allozymes by Joswiak (1980), the separation time of the two clades (*erythrogaster* and *brachyurus* clades) in the genus *Phoxinus* was estimated about 14 million years ago which would conform to the age of the Miocene.

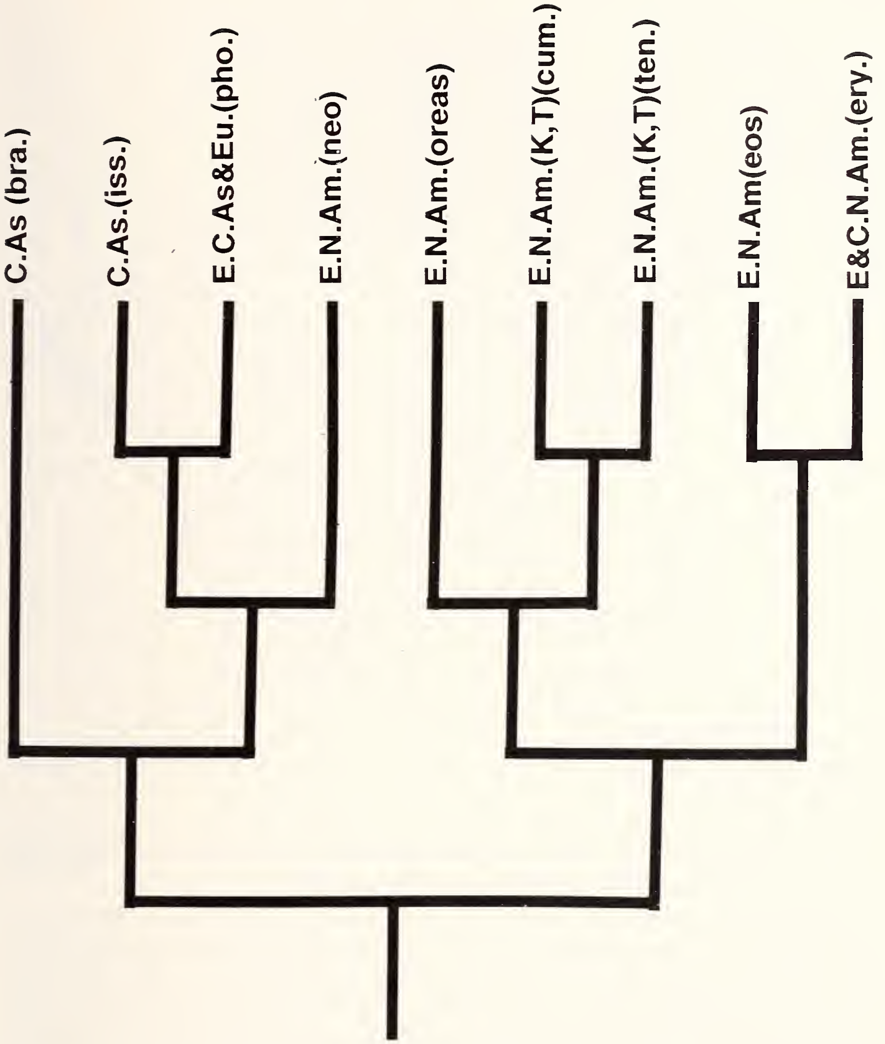

Fig.94: The area diagram of *Phoxinus*, based on the geographic distribution of each species of the genus and the phylogenetic hypothesis of the genus (Fig.93). The abbreviations of the regions are: C.As.: Central Asia; E. & C.N.Am.: east and central North America; E.C.As&Eu.: east and central Asia, and Europe; E.N.Am.: east North America; K.T: states of Kentucky and Tennessee of USA. The name in the parentheses corresponds to the species of *Phoxinus* occurring in the region: bra.: *Phoxinus brachyurus*; cum.: *P. cumberlandensis*; eos: *P. eos*; ery.: *P. erythrogaster*; iss.: *P. issykkulensis*; neo.: *P. neogaeus*; oreas: *P. oreas*; pho.: *P. phoxinus*; ten.: *P. tennesseensis*.

The Asian portion of the ancestor of *Phoxinus* became the ancestor of the *P. phoxinus* clade. This portion was split into *P. brachyurus* and the ancestor of the *P. phoxinus* species complex. How this event happened needs to be better understood. *P. brachyurus* occurs

Fig.95: Composite distribution for the ranges of species of *Phoxinus* in North America. (Data summarized from Lee et al. 1980.)

only in a small area of Illi River of Xinjiang (China) and of Kazakhstan in Asia (Berg 1949, Yang & Huang 1964, Reshetnikoo & Shakirova 1993).

I hypothesize that the ancestor of the *P. phoxinus* complex might have occurred in Asia and dispersed from Asia into North America through the Bering land connection in (or before) the Pliocene, otherwise it would be difficult to interpret the origin of *P. neogaeus*. The ancestor of *Phoxinus* species complex is proposed to have been separated into Asian portion and North American portion, by the submission of the Bering land connection during the Pliocene. The alloelectrophoretic studies on allozymes of *Phoxinus* (Joswiak 1980) showed this separation might have taken place about eight million years ago. The Asian portion of the ancestor was speciated into *P. issykkulensis* which occurs only in Lake Issyk-ku of Kazakhstan, and *phoxinus* which occurs in Asia and Europe. The fish fauna in the Lake Issyk-kul shows that the Lake Issyk-kul was isolated from its surrounding (Reshetnikoo & Shakirova 1993) though when and how the isolation occurred is uncertain. The speciation of the ancestor of "*P. phoxinus* + *P. issykkulensis*" might be related to this vicariant event.

The North American portion of the ancestor of the *Phoxinus* species complex was speciated into *P. neogaeus*, which prefers to live in boggy environment. *P. neogaeus* now oc-

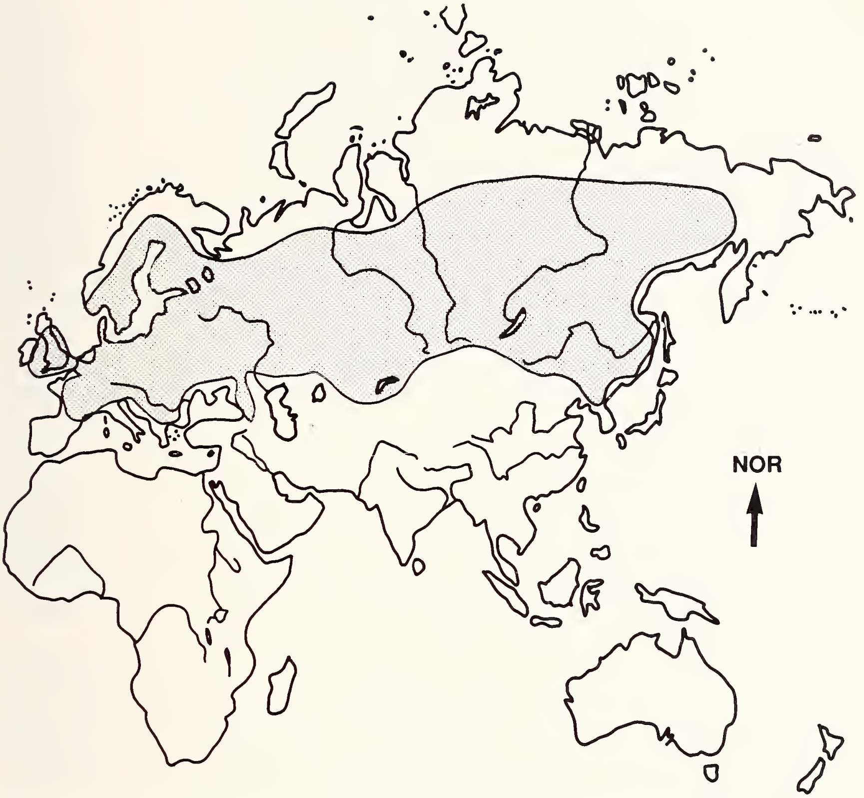

Fig.96: Composite distribution for the ranges of species of *Phoxinus* in Eurasia (data summarized from Berg 1949, Banarescu 1964, Yang & Huang 1964).

curs in the northern portion of North America. Some isolated populations are present in central Wisconsin (Green 1935), South Dakota (Evermann & Cox 1896a, Churchill & Over 1938), Nebraska, Colorado, and Wyoming (Bailey & Allum 1962). (See the species account of *P. neogaeus* below.) The isolated populations indicate *P. neogaeus* used to have a much broader geographic range. These isolated populations might be the descend from glacial populations that failed to expand following the deglaciation (Underhill 1957), or due to the similar causes for the isolated populations of *P. erythrogaster* discussed by Cross (1970) (see below). Mahy (1975c) interpreted the present distribution of *P. neogaeus* as northern dispersal of the species from its refuge.

The Pleistocene glaciation in North America during which ice covered the area to 40° (N. lat.) played an important role in the current geographical distribution of the North American freshwater fishes (Underhill 1957, McPhail 1963, Cross 1970). During the glacial advances, the range of fishes in the area covered by the ice were forced to southward, except some may have persisted in refuge that remained ice-free. The current geographical distribution of *Phoxinus* in North America exemplifies this. The North American portion of the ancestor of *Phoxinus* became the ancestor of the *erythrogaster* clade after its isolation from Asia in the Tertiary. The *erythrogaster* species pair (*P. eos* and *P. erythrogaster*) speciated from their ancestor probably by the adaptation to different habitats, or by some vicariant event. *P. eos* prefers a boggy environment, whereas *P. erythrogaster* lives in headwater or spring habitats. *P. eos* has a northern distribution not overlapping the range occupied by *P. erythrogaster*, but partially covering the geographic distribution of *P. neogaeus*. *P. erythrogaster* is distributed from Maine and Western Pennsylvania to Arkansas and Alabama, and a few isolated populations are present in Tennessee, Kansas, Colorado, and New Mexico (Koster 1957; Cross 1970). (See the species account of *P. erythrogaster* below).

These isolated populations of *P. erythrogaster* indicate this species once had an extensive southwestern distribution (Cross 1970). Because *P. erythrogaster* usually occurs in headwater or spring habitats, Cross (1970) interpreted the current distribution of this species caused by "(1) southward dispersal (of the species) during glacial advances, due to atmospheric cooling and consequent cooling of streams, probably supplemented by increased moisture and more consistent flow; (2) subsequent extirpation of most southern populations as atmospheric temperatures became warmer, heating the shallower streams and causing many of them to dry, but leaving remnant populations of these species near springs." (Cross 1971:251). The isolated populations of *P. eos* and *P. neogaeus* might be interpreted in a similar manner (Cross 1971).

The ancestor of the *oreas* species complex was hypothesized to have been distributed in the eastern portion of the preglacial Teays River drainage (Starnes & Jenkins 1988). This speciation event might be caused by the "capture of an upper Teays (New River) tributary by an upper Tennessee River (Holston River) tributary" (Starnes & Jenkins 1988:527).

TAXONOMY OF *PHOXINUS* RAFINESQUE, 1820a

Synonymy

Phoxinus Rafinesque, 1820a: 236 (type species: *Cyprinus phoxinus* Linnaeus, 1758: 322; Europe).

Chrosomus Rafinesque, 1820a: 237 (type species: *Luxilus erythrogaster* Rafinesque, 1820a: 237; Kentucky, USA).

Phoxinus Agassiz, 1835: 37 (type species: *Cyprinus phoxinus* Linnaeus, 1758: 322; Europe).

Eulinneella Dybowski, 1916: 101 (type species: *Cyprinus phoxinus* Linnaeus, 1758: 322; Europe).

Pfrille Jordan, 1924: 71 (Type species: *Phoxinus neogaeus* Cope, 1869: 375, in Günther 1868; New Hudson, Livingston County, Michigan, USA).

? *Acahara* Jordan & Hubbs, 1925: 177 (type species: *Richardsonius semotilus* Jordan & Starks, 1905; Japan).

Parchrosomus Gasowska, 1979: 404 (type species: *Chrosomus oreas* Cope, 1868: 233; Virginia, USA).

Discussion on the Synonymy of *Phoxinus*

The synonymy of *Phoxinus* differs with the views of various authors. Thus the content of the genus changed from time to time. The synonymy used most are those of Berg (1949), Banarescu (1964), and Howes (1985).

Synonymies in Banarescu (1964) and Howes (1985) are modified from those by Berg (1949). *Gila* of North America in the synonymy of Berg (1949) was removed and considered a distinct taxon (Miller 1945; Uyeno 1960). *Eulinneela, Lagowskiella, Eupallasella*, and *Czekanowskiella* were deleted from, and *Chrosomus* was added to, the synonymy in Berg (1949) by Banarescu (1964). Howes (1985) reviewed the synonymy of Berg (1949) and Banarescu (1964), and generally agreed with Banarescu (1964), except for deletion of *Phoxinus* of Agassiz, *Rhynchocyprin*, and *Moroco* from, and adding of *Eulinneella*, ?*Acahara*, and *Parchrosomus* to the synonymy of Banarescu (1964).

The synonymy of *Phoxinus* proposed herein agrees with those of Howes (1985), except the differences shown in Tab.2. I have not had the opportunity to study the species of *Acahara* (*A. semotilus*), and thus, I follow Howes (1985) in listing this name as a synonym of *Phoxinus* with a question mark (?) indicating the uncertainty.

Tab.2: Differences between the synonymy of *Phoxinus* by Howes (1985) and this study.

Howes (1985)	This Study	Reasons for Change
Chrosomus Rafinesque 1820b:47	*Chrosomus* Rafinesque 1840a:236	Rafinesque (1820a) might appear earlier than Rafinesque (1820b). See „Historical Review of *Phoxinus*“ of this study.
Type species of *Chrosomus*: *Chrosomus erythrogaster* Raf.	Type species of *Chrosomus: Luxilus erythrogaster* Rafinesque: 1820a:237	*Chrosomus erythrogaster* Raf. was originally described as *Luxilus erythrogaster* Raf.
No *Phoxinus* Agassiz 1835	With *Phoxinus* Agassiz 1835	*Phoxinus* Agassiz 1835 is a synonym of *Phoxinus* Rafinesque 1820a because both were typed by the same species: *Cyprinus phoxinus* Linnaeus
Type species of *Eulinnella: Phoxinus phoxinus* Linn.	Type species of *Eulinnella: Cyprinus phoxinus* Linnaeus	*Phoxinus phoxinus* was originally described as *Cyprinus phoxinus* by Linnaeus (1758)

Diagnosis (emended from Rafinesque 1820a, Berg 1949, Banarescu 1964, and Howes 1985)

Small size, less than 100 mm in SL in most species; body elongate; no barbel; Eurasian species bearing two rows of pharyngeal teeth, and silver peritoneum; North American species bearing one row of pharyngeal teeth (except *Phoxinus neogaeus* with two rows) and dark peritoneum; in young, side with one horizontal dark stripe; in adults, side with at least one longitudinal dark stripe, or about 10 vertical dark bars (*P. phoxinus*); the lateral stripe interrupted or not; supraorbital canal interrupted between nasal and frontal bones; preoperculomandibular canal interrupted into mandibular and preopercular segments; preopercular canal ending at middle of the ascending arm of the preopercle; scales small; in breeding males, breast scales deeply embedded and bearing a series of tubercles at their apical margins; scales on caudal peduncle bearing three or more tubercles at apical margin; orbital septum low; pharyngeal pad of basioccipital bone bearing an anterior process; nasal bone reduced, far from the anterior frontal canal opening; posttemporal fossa small; supraoccipital crest small; supraoccipital anterior margin bearing one anteriorly directed process; vertebrae about 40.

Etymology

Phoxinus is a Greek word for an unknown river fish (Pflieger 1975), meaning tapering (Nelson & Paetz 1992). The name might refer to body shape of the species in the genus.

Composition

Nine species are included in the genus, i.e., *P. brachyurus, issykkulensis, neogaeus, phoxinus, erythrogaster, eos, cumberlandensis, oreas*, and *tennesseensis*. I am not certain at the present whether "*P. tchangi* Chen" should be included in the genus because I did not have opportunity to study the specimens of this species during this project. "*P. sedelnikowi* Berg, 1908" was listed as a species of *Phoxinus* by Howes (1985), though he did not study specimens of this species. Whether *P. sedelnikowi* belongs to the genus is an open question because I could not get specimens of the species, and published data about this species are scant.

Distribution

Species of *Phoxinus* occur in North America and Eurasia (Figs.95, 96). See below for the distribution of each species in the genus.

Classification of *Phoxinus*

According to the phylogenetic hypothesis of *Phoxinus* proposed herein (Fig.93) and the phylogenetic listing convention proposed by Wiley (1979, 1981) and Wiley et al. (1991), the classification of *Phoxinus* is arranged as follows:

- Genus *Phoxinus*
  - *brachyurus* clade
    - *P. brachyurus* Berg
    - *phoxinus* species complex
      - *phoxinus* species pair
        - *P. issykkulensis* Berg
        - *P. phoxinus* (Linnaeus)
      - *P. neogaeus* Cope
  - *erythrogaster* clade
    - *oreas* species complex
      - *P. oreas* (Cope)
      - *cumberlandensis* species pair
        - *P. cumberlandensis* Starnes & Starnes
        - *P. tennesseensis* Starnes & Jenkins
    - *erythrogaster* species pair
      - *P. eos* (Cope)
      - *P. erythrogaster* (Rafinesque)

Key to the species of *Phoxinus*

1.	Intestine shorter than standard length, simply coiled; pharyngeal teeth in two rows; most occurring in Eurasia (only *P. neogaeus* in North America)	2.
	Intestine longer than standard length, coils complex; pharyngeal teeth in one row; all occurring in North America	5.
2.	Peritoneum dark; mouth opening large, extending to middle of pupil, occurring in North America	*P. neogaeus*
	Peritoneum silver, mouth opening small, extending to the anterior margin of orbit, occurring in Eurasian	3.
3.	Side with about 10-15 vertical bars; genital papilla well developed with an elongate posterior process in adult of both sexes; dorsal margin of epibranchial 4 deeply forked	*P. phoxinus*
	Side with one longitudinal stripe, without vertical bars; genital papilla small, without posterior process; dorsal margin of epibranchial 4 not deeply forked	4.
4.	Air bladder short and broad	*P. issykkulensis*
	Air bladder slender	*P. brachyurus*
5.	Opercle narrow and elongate	*P. cumberlandensis*
	Opercle broad and short	6.
6.	Dentary relatively short and blunt; pharyngeal bone with two large fossae, without small fossae	*P. eos*
	Dentary relatively elongate and slender; pharyngeal bone with more than two fossae, both large and small fossae present	7.

7. Sides bearing only one continuous longitudinal stripe (unbroken); posterior process of basioccipital bone broad and stout . . . . *P. tennesseensis*
   Side with broken longitudinal stripe(s); posterior process of basioccipital narrow and slender . . . . 8.
8. Side with one longitudinal stripe and a few vertical bars; isthmus and breast dark; intestine length more than 2.5 times standard length . . . . *P. oreas*
   Side with two longitudinal stripes without vertical bars; isthmus and breast with few or no melanophores; intestine length about 2 times standard length . . . . *P. erythrogaster*

SPECIES ACCOUNTS

Phoxinus phoxinus (Linnaeus, 1758)

Synonymy

Cyprinus aphys Linnaeus, 1758 – Linnaeus 1758: 323 (orig. desc.; type locality: Europe)[1]; Tack 1940a: fig.17 (larva); Wheeler 1991: 163 (type specimens in the Zoological Museum of the University of Uppsala).

[1]) Abbreviations used in the synonymy are as follows: desc.: description; dist.: distribution; orig.: original; mis.id.: mis-identification.

Cyprinus phoxinus Linnaeus, 1758 – Linnaeus 1758: 322 (orig. desc.; type locality: Europe); Agassiz 1835: 37 (name); Jordan 1890: 50 (name); Jordan 1924: 71 (name); Mahy 1975c: 618 (name); Gasowska 1979: 371 (name).

Phoxinus laevis Agassiz – Agassiz 1835: 37 (orig. desc.; type locality: Europe); Cope 1869: 375 (name); Berg 1905: 196 (name); Nigrelli 1934: 64 (name); Bullough 1940: figs.1-14 (sexual reversal); Harrington 1950: 306, 309 (name); Medlen 1951: 149 (name); Rough 1954: 191 (name); Holz & Weber 1970: 1349, 1350 (nerve fibers in olfactory bulb); Wiley & Collette 1970: 170 (name); Mahy 1975a: 29 (name).

P. phoxinus Linnaeus – Starmach 1963: 367-368, tabs. I, II, IV , figs.1, 1-7, 10 (morphology); Strâskraba et al. 1966: 304 (name); Gentle 1971a: 83, 90, tabs.1-2, figs.1, 2 (color change); Gentle 1971c: 641, tab. 1, figs.2-7 (color change); Gentle 1972a: 701, tabs. 1-2 (physiology, color change); Gentle 1972b: 709, 711 (physiology).

P. phoxinus (Linnaeus) 1758 – Berg 1906: 197, 212 (dist., Russia); Cockerell 1909: 216 (scales); Frost 1943: 139, tabs.1-7, figs.1-9 (life history); Frost 1946: 224 (diet); Jones 1956: 271 (behaviour reaction to light intensity); Banarescu 1964: 333-343, figs.142, 143 (whole body), 144 (dist., Asia, Europe); Berinkey 1968: 275, tabs.I -IV (population variation); Wiley & Collette 1970: 168, 170 (tubercles); Kulamowicz & Korkuc 1971: 299, 301, tabs.1-2 (Morphology); Mann 1971: 155, 166, tabs.13-14 (population); Gentle 1971a: 83, 90, figs.1-4 (color change); Gentle 1971b: 93, 102, figs.1-8 (color change); Mahy 1972: 728 (name); Maitland 1972: 852 (name); Pitcher 1973: 841 (schooling behaviour);

Volkova 1973: 592 (behaviour, Lake Baikal); Kennedy & Pitcher 1975: 454, fig.1 (homing behaviour); Mahy 1975a: 29 (name); Mahy 1975b: 179 (name); Mahy 1975c: 617-641, figs.1-21, 23B (osteology); Howes 1978: 4 (name); Settles & Hoyt 1978: 296 (name); Wheeler 1978: 130, 132, fig.on p.131 (whole body) (Northern Europe); Gasowska 1979: 371, 373, 377, 379, 381, 384-386, 388-390, 392-393, 399-402, figs.1, 9, 16, 22, 28, 35, 41, 47, 53, 57, 66, 74, 78, 87, fig.1 of p.11 (osteology); Stott & Buckley 1979: 135 (behavior); Wootton & Mills 1979: 607, 608, 611, 616, fig.I (physiology); Joswiak et al. 1980: 915 (name); Joswiak 1980: 2, 8, 12, 15, 17, 18, 22, tabs.4-5, fig.2 (chromosomes); Partridge 1980: 68, 69, tab.1, figs.1-9 (schooling behavior); Wootton et al. 1980: 695-697, 704, tab.II, fig.2 (daily food consumption); Heese 1981: 67-75, tabs.1-4, figs 1, 2 (external morphology, Poland); Kennedy 1981: 621, figs.1-3 (homing behavior); Coad 1984: 135, tab.1, figs.1, 2 (specimens with deformed vertebral column); Constantinescu et al. 1984: 267, 284, 286, tab.1, figs.1-10, 12 (breeding coloration, behavior, Romania); Heese 1984: 25, 28, 34, tabs.1-3, figs.2-9, pls. 1-4 (biology, Poland); Legkiy & Popoya 1984: 72-79, tab.1 (behavior); Banbura 1985: 235, fig.2 (two deformed species without pectoral fin); Dauod et al. 1985: 3, figs.2-10 (population structure, diet); Pfeiffer et al. 1985: 553, 555, 558-559, 562-563, 565-567, 569, tabs II-VI , figs.1-12 (alarm substance); Kim & Kang 1986: tabs.1-2, figs.14c, 15b, 16c (osteology); Magurran & Girling 1986: 510 (behavior); Magurran 1986: 159, fig.1 (schooling and shoaling behavior); Pitcher & Turner 1986: 59, 60 (schooling behavior); Pitcher, Green & Magurran 1986: 439 (behavior); Pitcher et al. 1986: 83 (schooling); Cavender & Coburn 1987: 1 (name); Mills 1987: 53, tab.1, figs.1-10 (life history, Dorest, UK); Rasotto et al. 1987: 51, 53, 56, tabs.I-II , figs.1-10 (sexual inversion); Cuvin & Furness 1988: 205, figs.1-4 (toxicology); Doadrio & Garzón 1988: 389, 390, fig.1 (new record, Iberian Peninsula, Spain); Levesley & Magurran 1988: 699, fig.1 (alarm substance reaction); Cui & Wootton 1988a: 749, 750, tabs.I-VI, figs.1-4 (physiology); Cui & Wootton 1988b: 431, tabs.I-III, figs.1-4 (physiology); Banarescu 1989: 92, fig.2 (dist. map Eurasia); Bogutskaya 1989: fig.1a (infraorbital bones); Cui & Wootton 1989: 47-48 (physiology); Jeon 1989: 17, 29, 30, fig.10 (Korea); Travers 1989: 198, fig.18 (whole body) (dist., Mongolia); Chereshnev 1990: 113 (northeastern USSR); Banarescu & Coad 1991: 135, 143, 145, 147, 149 (Eurasian); Wheeler 1991: 163 (type specimen).

P. phoxinus (Linné, 1758) – Berg 1949: 123-126, figs.346 (whole body), 347 (whole body) (description, Eurasian).

P. phoxinus colchicus Berg, 1949 – Berg 1949: 126, fig.348 (western Transcaucasia).

P. p. phoxinus Linnaeus – Kulamowicz & Korkuc 1971: 302 (name); Haimovice & Ciuca 1973: 201-202, figs. 1-3. (Karyotype, 2N=52).

P. p. phoxinus (Linnaeus) – Banarescu 1964: 339-343 (Romania).

P. phoxinus ujmonensis Kaschtschenko – Berg 1949: 127, fig.349 (whole body) (Altai, Lake Teletskoe).

Material studied

AMNH 36873sw, 2 C&S; River Thames and tributary to River Kew, Middlesex County, England; R. P. Vari, and J. Jones; 11 September 1977. – AMNH 71940, 11 alch.; Frame

River, Wareham, Dorset County, England; A. Wheeler; 22 April 1982. – ANSP 6342, 1 alch.; England; collector unknown; date unknown. – ANSP 6343, 8 alch.; Mediterranean, Italy; C. L. Bonaparte; date unknown. – ANSP 82449, 4 alch.; Red Lake, Transilvania, Romania; A. Popescu-Gorj; 20 August 1956. – ANSP 105676, 2 alch.; Chihi, China; collector unknown; August 1932. – ANSP 153914, 10 alch.; Torrenete Stura di Lanzo, Cirie comm., 2 km upstream bridge on the road Cirie-Robassonero, Torino Province, Italy; M. Bani; 27 April 1984. – CAS (SU) 06383, 10 alch.; Herault Dept.-Sete, France; E. Moreau; date unknown. – CAS 48106, 36 alch.; 45 km N of Bucuresti: brook Muciucatu, tributary to Prahova River between villages of Tinosu and Crivina, Romania; P. Banarescu and Damian; 7 April 1981. – CAS 58633, 15 alch.; pond near Torrente Malone, 1 km upstream bridge on road Rivarossa-Argentera, Rivarossa comm., Torino Province, Italy; G. A. C. Balma; 13 November 1985. – FMNH 80685, 12 alch.; River Moldova at Fundul-Moldovei, Bucovina, Romania; P. Banarescu; 6 November 1968. – FRLM, 9508, 1 alch.; Altay, Xinjian, China; collector unknown; 6 June 1989. – FRLM, 9513, 1 alch.; Altay, Xinjian, China; collector unknown; 6 June 1989. – FRLM, 9515, 1 alch.; Altay, Xinjian, China; collector unknown; 6 June 1989. –KU 22850, 16 alch.; upper Maritza River at Kostenetz, Bulgaria, Romania; P. Banarescu; 2 September 1965. – KU 22853, 10 alch.; Taria Brook, tributary to Minis River, 6 km upstream from Bozovici, Romania; P. Banarescu; 23 July 1968. – KU 22854, 10 alch.; Minis River, Banat, Romania; P. Banarescu; 23 July 1968. – KU 22855, 10 alch.; Humorul Brook, Gura Humorului, Romania; P. Banarescu; 7 November 1968. – KU 22856, 4 alch. and 1 C&S; Maciucatul Brook, tributary to Prabova River, 43 km North Bucuresti, Romania; P. Banarescu; 17 April 1981. – KU 22857, 11alch.; Aries River at Cimpeni, Transylvania, Romania; P. Banarescu; 2 November 1989. – KU 22858, 86 alch.; Timis River at Carasebes, Romania; P. Banarescu; 11 June 1990. – KU 22859, 5 alch.; Lake Lacul Rosu on 'Bicaz River at Bicaz, Transylvamia, Romania; A. Popescu-Gori; date unknown. – KU 22860, 12 alch. and 2 C&S; probably Lake Lacul Rosu, Transylvania, Romania; collector unknown; date unknown. – MCZ 2049, 21 alch.; Lake Neuchatel, Switzerland; L. Agassiz; March 1860. – MCZ 18624, 12 alch.; Europe; C. Gegenbaur; date unknown (recorded in 1864). – MCZ 32372, 25 alch.; Teploje Lake, Bira River, basin of Amur, USSR, Asia; Vlad. Fish. Res. Sta.; 19 April 1927. – MHNG 658.86, 5 alch.; locality unknown; E. Galopin; date unknown. – MHNG 1503.52-55, 4 alch.; département de la Haute-Savoie, rivière des Usses, Prè S de Seyssel, France; P. J. Haymoz; 16 November 1974. – MHNG 2012.95-97, 3 alch.; Nery, La Repetance, La Laire, à Chancy, Genève, Switzerland; Stotz-Régnier; 9 May 1979. – MHNG 2082.41-46, 6 alch.; ruisseau Poenari, à tinosu, à 50 km, au Nord de Bucuresti, Romania; P. Banarescu and S. Damian; 7 April 1981. – USNM 204166, 10 alch.; River Mures at Deda, Transylvania, Romania; P. Banarescu; 19 October. – USNM 218523, 21 alch.; Lotru River, tributary to Olt River, at Brezmi, district Vilcea, Romania; P. Banarescu; 16 September 1969. – USNM 271535, 80 alch.; Moraca River and adjacent ponds, the Aluminum Plant, Crana Gora, Czechoslovakia; Knapp and Jacobi; 1 June 1973. – ZFMK 649-653, 656, 7 alch.; 1888. – ZFMK 631, 1 alch.; 8 April 1900. – ZFMK 798, 2 alch. – ZFMK 585-586, 2 alch.; May 1957. – ZFMK 660, 1 alch.; 19 August 1933. – ZFMK 657—659, 3 alch.; 1873. – ZFMK 1780, 1 alch.; 1969. – ZIL uncat. 8 alch.; Kolyma River, Russia; collector unknown; date unknown. – ZMH 15147, 10 alch.; Treen Schleswig-Holstein, Germany;

G. Duncker; 12 July 1926. – ZMH uncat., 3 alch.; Albaum near Altenhundem-Lennestadt, Germany; collector unknown; 16 October 1991. – USNM 276160, 10 alch.; T. stura di Lanzo, Cirie Comm., Toprino Prov., 0.5 KM upstream bridge on the Road Cirio Robassomero, Italy; M. Banio; 27 April 1984.

Diagnosis (amended from Berg 1949, Yang & Huang 1964)

Primary lamellae in olfactory organ 15; no longitudinal lateral stripe; more than 10 vertical bars on side in adults (in young, vertical bars absent, but lateral stripe present on sides); body lateral line complete. Breast scales bearing tubercles in breeding females. Tubercles on dorsum of head large and few; 4 or 5 large tubercles on dorsal rim of orbit; very high density of tubercles on opercle; tubercles present on caudal fin in breeding female; gas bladder slender; intestine short; peritoneum silver; pharyngeal teeth in two rows.

Description (Tab.3)

An Eurasian species of *Phoxinus* with average standard length (adults) about 60 mm, maximum standard length of 125 mm (Berg 1949). Head large, broad, and robust; its length 25% of standard length; its width 51% of its length. Snout elongated, its length 28% of head length, 102% of orbit length. Eye lateral on head; orbit length 27% of head length.

Tab.3: Body proportions (%) of *Phoxinus phoxinus*. (ACGL: anterior chamber of gas bladder length; BD: body depth; BIW: bony interorbital width; CPD: caudal peduncle depth; CPL: caudal peduncle length; HD: head depth; HL: head length; HW: head width; IL: intestine length; Number: number of specimens; OL: orbit length; PCGL: posterior chamber of gas bladder length; PRDL: predorsal fin length; PRPL: prepelvic fin length; S: standard deviation; SL: standard length; SNL: snout length).

	HL/SL	HD/SL	BD/SL	CPL/SL	CPD/SL	PRDL/SL	PRPL/SL	IL/SL	HW/SL	HD/HL
Number	25	26	24	25	25	23	26	4	25	26
Range	23.2 – 27.0	15.3 – 21.6	18.8 – 22.8	23.3 – 28.2	7.7 – 10.1	52.9 – 59.0	42.5 – 50.2	65. 4 – 76 .2	11.7 – 13.9	14.1 – 17.4
Mean	25.3	16.3	20.3	25.6	9.2	55.6	47. 1	70.0	12.9	16.3
S(±)	1.0	1.5	1.6	1.6	0.8	1.8	2.1	5.0	0.7	1.5

	OL/HL	HW/HL	SNL/HL	BIW/HL	BIW/OL	SNL/OL	PRDL/ PRPL	CPD/CPL	ACGL/ PCGL
Number	22	20	25	25	23	22	24	25	3
Range	23.2 – 31.8	48.2 – 51.3	21.5 – 34.2	26.3 – 35.2	116.7 – 120.5	79.2 – 121.6	115.1 – 122.1	29.0 – 40.0	45.0 – 54.3
Mean	26.7	49.5	28.1	32.1	118.8	102.3	119.8	36.1	50.0
S(±)	3.3	1.6	2.9	3.4	2.5	14.7	7.3	3.0	4.5

Mouth small, slightly subterminal and oblique; mouth gape not extending to below the anterior margin of the orbit. Lower jaw slightly shorter than the upper one.

Bony interorbital space wide, its width 119% of orbit length and 32% of head length. Anterior nasal opening smaller and shorter than posterior nasal opening, the former about half the size of the latter. Entire margin of anterior nasal opening erect; margin of posterior nasal opening, except its anterior part, not erect.

In young individuals (25.3 mm standard length), axis of olfactory organ very short, oval in shape, and situated in anterior part of olfactory chamber; five primary lamellae present. In larger specimens (60.1 mm standard length), the axis elongated and extending to posterior portion of organ chamber; up to 16 primary lamellae present. Numerous melanophores present on primary lamellae in young, on both primary lamellae and axis in adult.

Body slender, not strongly compressed. Maximum body depth 20% of standard length. Caudal peduncle short and high, its length 26% of standard length, its depth 36% of its length.

In male, the genital papilla spheric in shape, and smaller than that in female. Surface of papilla smooth without small skin fold, but one large skin fold present in some specimens. Genital orifice large. Posterior projection of genital papilla well-developed, its posterior end far from origin of anal fin.

In female, genital papilla well-developed, its posterior margin with few well-developed projections; a long projection extending from posterior of papilla, reaching anal fin origin. Surface of papilla bearing developed skin folds.

Pectoral fin fan-like in male, sharper and smaller in female, its posterior margin reaching origin of pelvic fin in adults; 14-16 fin-rays. Origin of pelvic fin farther forward than origin of dorsal fin. and in anterior half of standard length; prepelvic length 47% of standard length; eight rays.

Dorsal fin originating behind pelvic origin, predorsal length 56% of standard length, and 120% of prepelvic length; with two procurrent rays, eight fin-rays. Anal fin originating below insertion of dorsal fin; with two procurrent rays and eight rays. Caudal fin deeply forked, lobes sharp; with 11 or 12 dorsal procurrent, 9-10 ventral procurrent rays, and 19 (10+9) principal rays.

Scales covering whole body, weakly embedded on lateral and dorsal surface of body, but deeply embedded on ventral side of the body.

Left and right supratemporal canals separated from each other, with four pores each side. Otic canal with five pores. Supraorbital canal without interruption, except the region between nasal and frontal bones, with nine pores. Infraorbital canal with 10 pores. Preopercular canal with eight pores. Mandibular canal with four pores. Body lateral line complete, extending to caudal fin base, number and positions of the pores varying individually; about 82 lateral line pored scales.

Pharyngeal bone robust; its pitted surface broad with four large fossae. Posterior limb elongate, slender and straight; anterior limb slender, narrowing posteriorly, expanding anteriorly, bearing a notch at anterior end. Pharyngeal teeth very strong, hooked at tip, in two rows, 2,4-5,2, 1,5-5,2, 1,4-5,1. Teeth in main row more developed than those on minor row. Masticatory surface of teeth round and smooth.

Vertebrae 40-43 (three specimens); precaudal vertebrae 22 or 23, caudal vertebrae 18 or 20.

Intestine short, simply looped; its length 70% of standard length. Gas bladder slender and elongated. Anterior chamber of the bladder round at its anterior end, and about 50% of the posterior chamber in length. Both chambers nearly cylindrical, not tapering from anterior to posterior portion, though posterior end narrows slightly. Constriction elongated. Pneumatic duct placed at middle of constriction. Peritoneum silver in color.

Male Tuberculation. Dorsal, lateral and ventral sides of the head bearing tubercles. However, the morphology and density of the tubercles vary with regions. On dorsum of head, tubercles few in number, but large and tall in shape. Three tubercles along the medial margin of nasal opening, two of which are adjacent to tubercles at the medial margin of the other nasal opening. Four tubercles on the dorsal rim of the orbit. The anterior two are close to each other, and posterior two also close together. Five tubercles dorsally between eyes, four of the five forming a square, the remaining one located at center of square. Tips of these tubercles directed left, right, posteriorly, or dorsally. About 14 tubercles arranged in three rows on posterior portion of head: anterior row of three, middle row of four, and posterior row of seven tubercles.

Numerous tubercles present on lateral side of head. Posterior one-third of opercle bearing small, tall, sharp tubercles; anterior area with larger, shorter tubercles. Density of tubercles on the opercle very high, the most dense among all regions in all studied *Phoxinus* species. Branchiostegals and cheek bearing numerous large but short tubercles. No tubercle on anterior end of snout. On ventral side of the head, tubercles mainly present at ventral portion of the lower jaw.

The dorsal, lateral, and most of the ventral sides of body bearing tubercles. About seven rows of scales on breast bearing well-developed tubercles. Each scale in this region bears a few tubercles at its apical margin to form a comb-like edge. Ventral body anterior to anal fin origin not bearing tubercles. Each scale on lateral and dorsal surfaces having four to 12 tubercles at apical margins.

All fins bear sharp tubercles. On ventral side of pectoral fin, membrane between two rays from the first to eighth rays bear four to seven tubercles in one row near the distal margin of the fin; fewer tubercles on fin-rays. On the dorsal side of pectoral fin, each ray from the second to eighth bears three rows of tubercles distally, decreasing to two rows and then to one row proximally. Fewer tubercles present on the membrane. No tubercles present at the proximal part of pectoral fin.

On the dorsal side of the pelvic fin, each of the first five rays bears two rows of tubercles distally, decreasing to one row proximally. The proximal one-third of the fin bears no tubercles. Each of the remaining rays bears one short row of tubercles on the proximal portion. No tubercles on interradial membranes of the fin. Fewer tubercles present on ventral side of fin.

Few tubercles are present on fin rays and membrane of the dorsal, anal, and caudal fins.

Female Tuberculation. Tubercles are present on dorsal and lateral sides of head, no tubercles on ventral side of head. Tubercles on dorsum of head few, large and sharp. Five large tubercles along dorsal rim of each orbit, two or three of the five at the anterodorsal side of snout. No tubercles present at anterior end of snout. Numerous small tubercles on lateral side of the head.

Each scale of the 11 rows of breast scales bearing four to eight small tubercles along the apical margin. Scales on the area between the breast scales also bearing tubercles. The remaining ventral area of body bearing no tubercles. No tubercles on all fins.

Coloration. 14-15 parallel and vertical dark bars present on side, from behind the gill cleft to posterior part of caudal peduncle. Bars in front of insertion of dorsal fin longer than those behind insertion. Juveniles (less than 25 mm standard length) lack vertical bars but have one longitudinal stripe from the gill cleft to the caudal fin base. Some specimens also bearing a few large speckles dorsally. A dark dorsal stripe present from nape to base of caudal fin.

Numerous melanophores are present on trunk, except ventral to lateral bars where melanophores are absent or few. Breast region bearing melanophores in male. Dorsum dark, with numerous melanophores, becoming paler on sides in spaces between lateral bars.

Head with numerous melanophores dorsally, laterally, and ventrally. Anterior part of opercle bearing more melanophores than its surrounding.

All fins bearing melanophores on rays and membrane. On pectoral fin, the first ray darker than others. Pelvic fin dark, evenly pigmented. Base of dorsal fin with a black patch, and the rays with more melanophores than the membrane. Anal fin uniformly dark, but base of fin bears very few melanophores. Base of caudal fin bearing more melanophores than rest of the fin.

Biology

P. phoxinus inhabits flowing water, ponds, shallow lakes, and margins of deep lakes, such as Lake Baikal (Berg 1949). It lives on various bottoms, but prefers stony substrates (Frost 1943). Schools of hundreds of individuals sometimes occurs in shoal area (Frost 1943, Partridge 1980). Fish species associated with *P. phoxinus* include freshwater eel [*Anguilla anguilla* (L.)], salmon (*Salmo salar* L.) (Frost 1943), stickleback (*Gasterosteus aculeatus* L.), and *Noemachielus barbatulus* (L.) (Dauod et al. 1985).

The food mainly consists of copepods, filamentous algae and diatoms. *P. phoxinus* also eats insect larvae (Frost 1943). Dauod et al. (1985) recognized 12 categories of food items for the species: surface insects, mollusca, trichopteran larvae, trichopteran pupae, cladocera, copepoda, chironomid larvae, chironomid pupae, ephemeropteran nymphs, other larvae, *Gammarus* and "chance" food. According to these authors, the diet composition changes seasonally. For instance, the most important food items early in year were chironomid larvae, mollusca, and trichoptern larvae. These foods were replaced by daphnia and surface insects in May.

The species reaches its mature at 35-45 mm standard length in about their second year (Dauod et al. 1985). The breeding season varies from early April to September depending partly on latitude. Prior to spawning, large school of adults migrates to smaller stream having cooler water (Bade 1902, Frost 1943). The school might be concentrated on an approximately circular surface of about 30 cm diameter, and 1.5 cm thick layer. Individuals in the school form a few breeding centers with the presence of females (Constantinescu et al. 1984). One or two (seldom three) males chase one female spawning (Constantinescu et al. 1984). The male contacted the female then flanked her. Males were also observed rotating two by two. Fecundity ranges from 700 to 1000 eggs. Diameter of a ripe unfertilized egg is about 1.3 mm (Berg 1949), that of an ovum is 1.0 to 1.4 mm (Dauod et al. 1985).

Distribution

P. phoxinus occurs in Europe, and east and central Asia. In Asia, it occurs in northern China to Helong Jiang River, Yalu River and Tumen River (Yang & Huang 1964), Korea (Mori 1928a, b, 1930, 1934, Jeon 1989), and Mongolia (Travers 1989). Banarescu (1964: fig.142) illustrated the geographic distribution of the species.

Comments

Bullough (1940) mentioned that the males were darker than females in *P. phoxinus*. Specimens studied herein, however, show little sexual difference in color. In some populations, females could be slightly darker than males. Frost (1943) showed no difference in color found between females and males.

The type specimen of *P. phoxinus* is problematic. The specimens labeled "*Cyprinus aphya*" (Catalogue no: ZIU 211) in the Zoological Museum of the University of Uppsala were generally regarded as the type series of *P. phoxinus* because *Cyprinus aphya* was usually considered a synonym of *P. phoxinus* (Wheeler 1991). However, these specimens are in poor condition and difficult to identify, and no evidence shows whether these specimens are the ones that Linnaeus used to describe *C. aphya*, or *Cyprinus phoxinus*, or neither (Wheeler 1991).

Etymology

The epithet *Phoxinus* was derived from Greek, means tapering (Nelson & Paetz 1992). It may refer to the body shape of the species.

Phoxinus brachyurus Berg, 1912

Synonymy

Phoxinus brachyurus Berg, 1912 – Berg 1912: 241, fig.16 (orig. desc.; type locality: Chilik River in the Ili basin, Kazakhstan); Berg 1932: 354, 365-366, fig.276; Berg 1949: 107, 121-122, fig.344 (Chilik River, Ili River; Basin of Chu River, Central Asia.); Yang & Huang 1964: 22, 24-25, fig.1-13 (Ili River, Xinjiang, China); Howes 1985: 71 (name).

Material studied

MCZ 3006: 2 alch. and 1 C&S; Siberia, Lake Baikal, USSR; J. D. E. Schmeltz, Jr.; 1873. – MMSU 3928: 1 alch; Russia; collection date unknown.

Diagnosis (amended from Berg 1949, Yang & Huang 1964)

A *Phoxinus* species with numerous dark blotches on sides of body; left and right supratemporal canal almost joined on the parietal; body lateral line interrupted; two medial extrascapulae on supraoccipital; anterior process of basioccipital absent; epibranchial 4 bearing an elongate dorsally directed process.

Description

An Asian *Phoxinus* species with maximum standard length of 90 mm. Head large, laterally compressed, its length 24% of standard length, its width 13% of its length. Snout moderately elongate, slightly shorter than orbit length in adult, or equal in young; its length 22% of head length, and 92% of orbit length. Eye large. Mouth terminal and moderately large; mouth gape not extending to below anterior margin of the orbit; lower jaw equal to upper in length. Bony interorbital space relatively narrow.

Axis of olfactory organ elongate, elliptical; ten primary lamellae in the olfactory organ. Melanophores present on both primary lamellae and axis. No data available for young individuals.

Body elongate, moderately deep, not strongly compressed; round at abdomen. Dorsal profile slightly arched. Maximum body depth 21% of standard length. Ventral profile nearly horizontal. Caudal peduncle short and high, its length 19% of standard length, its depth 54% of its length.

Genital papilla short and small, without posterior process; much more developed in breeding season than in nonbreeding season (Yang & Huang 1964).

Pectoral fin small and short; its posterior margin forward from base of pelvic fin; fin-rays 13-14. Pelvic fin small, acute at distal end, not reaching the vent; fin-rays eight (two specimens), or seven (one specimen). Dorsal fin round, originating posterior to the pelvic fin base; with one or two procurrent rays and eight rays. Anal fin small and round, its origin slightly posterior to insertion of dorsal fin; with one or two procurrent rays, eight fin-rays. Caudal fin shallowly forked, its lobes round; dorsal procurrent rays six or seven, ventral procurrent rays five or six, principal rays 19 (10+9).

Left and right supratemporal canals near to (but not connected) each other at supraoccipital bone, with 5-8 pores. Otic canal with four or five pores. Supraorbital canal interrupted, with 9 or 10 pores. Infraorbital canal interrupted, with 11 (one specimen) or 13 (two specimens) pores. Preopercular canal complete, with 10 pores. Mandibular canal with seven pores. Body lateral line straight, interrupted, extending to base of caudal fin. Entire abdomen scaled.

Pharyngeal bone slender, its posterior limb slightly bent. Pitted surface narrow with four major fossae. Pharyngeal teeth in two rows: 5.2-1.4. Teeth slender, hooked at tip; masticatory surface of teeth round and smooth.

Vertebrae 38-40; precaudal vertebrae 20-21, caudal vertebrae 18-19.

Intestine shorter than standard length, simply looped, its length 75% of standard length (one specimen). Gas bladder relatively slender, anterior chamber 62% of the posterior one in length (one specimen); pneumatic duct connecting with anterior portion of the posterior chamber. Peritoneum silver in color.

Tuberculation – No data about tuberculation of this species was available at the present.

Coloration – One lateral stripe present at middle of the sides of the body, extending from upper end of gill cleft to caudal fin base; stripe faint anteriorly. Melanophores present on whole body except breast and isthmus, though lighter at ventral portion than at dorsal portion of trunk. Numerous dark speckles (smaller than pupil in diameter) present dorsally on the sides of the body (dorsal of the lateral dark stripe). A mid-dorsal dark stripe present, extending from nape to base of caudal fin.

Biology

Spawning season is in March and April (Berg 1949). No other data available.

Distribution

P. brachyurus is restricted to the drainage of the Ili River in Kazakhstan, and the Xinjiang Uygur Autonomous Region in China.

Comments

Yang & Hung (1964) mentioned that this species lacks scales on the abdomen. Berg (1949) and my observation showed that the entire ventral side of the body is scaled.

Etymology

The epithet "*brachyurus*" might be derived from a combination of "brachy-" meaning "short" and "-urus" meaning "tail" (C.R. Robins 1995; pers. comm.).

Phoxinus issykkulensis Berg, 1912

Synonymy

Phoxinus issykkulensis Berg, 1912 – Berg 1912: 243, fig.7 (orig. desc.; type locality: Lake Issy-kul, Kazakhstan); Berg 1932: 366, fig.27 (desc., Issyk-kul River and tributaries, Kazakhstan); Berg 1949: 122, 123, fig.277 (Lake Issykyl's tributaries, Kazakhstan); Howes 1985: 71 (name).

Material studied

NMC 77-0883 (originally from the Zoological Institute, Academy of Sciences, USSR, Cat. No. 26374), 3 alch.; Brook mouth, Lake Issyk-kul, Jamy-Uguz, USSR; D. Pedashenxo; 1909. – MMSU 10696 1 alch. and 1 C&S.. – ZIL 26373 (3), 3 alch; Lake Issyk-kul; collector unknown; date unknown.

Diagnosis (amended from Berg 1949)

Caudal fin deeply forked, its lobes pointed; anteromedial process of maxilla absent; pharyngeal 2+3 triangular in shape; gas bladder broad and short.

Tab.4: Body proporations (%) of *Phoxinus issykkulensis.* (ACGL: anterior chamber of gas bladder length; BD: body depth; BIW: bony interorbital width; CPD: caudal peduncle depth; CPL: caudal peduncle length; HD: head depth; HL: head length; HW: head width; IL: intestine length; number: number of specimens; OL: orbit length; PCGL: posterior chamber of gas bladder length; PRDL: predorsal fin length; PRPL: prepelvic fin length; S: standard deviation; SL: standard length; SNL: snout length).

	HL/SL	HD/SL	BD/SL	CPL/SL	CPD/SL	PRDL/SL	PRPL/SL	IL/SL	HW/SL	HD/HL
Number	7	6	6	7	6	7	6	1	7	6
	26.4	16.6	23.3	18.0	9.0	53.4	48.2	–	12.8	59.3
Range	–	–	–	–	–	–	–	–	–	–
	30.0	18.3	25.5	23.9	10.4	59.7	54.1	–	15.1	63.5
Mean	28.1	17.1	24.4	21.5	9.9	58.0	52. 3	89.2	13.8	60.9
S(±)	1.1	0.6	1.1	1.8	0.5	2.7	1.9	-	0.9	1.5

	OL/HL	HW/HL	SNL/HL	BIW/HL	BIW/OL	SNL/OL	PRDL/ PRPL	CPD/CPL	ACGL/ PCGL
Number	7	7	7	7	5	6	7	7	1
	21.2	47.3	22.2	25.5	104.0	92.0	102.1	40.4	–
Range	–	–	–	–	–	–	–	–	–
	31.9	53.3	27.2	36.1	117.1	116.7	115.8	57.8	–
Mean	25.9	49.2	25.2	30.7	109.2	104.5	110.3	46.4	81.1
S(±)	4.0	2.7	1.8	3.3	6.0	11.6	5.4	6.1	–

Description (Tab.4)

An Eurasian *Phoxinus* species with maximum standard length of 102 mm (Berg 1949). Head large and elongate; laterally compressed, its length 28% of standard length, its width 61% of its length. Snout elongate, its length 25% of head length, and 105% of the orbit length. Eye relatively small, orbit length 26% of head length. Mouth small oblique, subterminal, extending to below anterior margin of eyes. Lower jaw slightly shorter than upper one.

Bony interorbital space relatively narrow, its width 109% of orbit length, and 31% of head length.

Axis of olfactory organ a long ellipse in shape. Primary lamellae about 10.

Body elongate, not strongly compressed, round at abdomen. Dorsal profile slightly arched, maximum depth 24% of standard length. Caudal peduncle deep, short and laterally compressed; its length 22% of standard length, its depth 46% of its length.

Genital papilla short, moderately developed, without a projection; its posterior end almost reaching anal fin origin.

Pectoral fin small and short, its posterior margin far away from the pelvic fin base, reaching about half-way between bases of pectoral and pelvic fins; with 14 or 15 fin-rays. Pelvic fin small, not reaching vent, with eight rays.

Dorsal fin round, with one procurrent ray and eight rays. Anal fin small and slightly pointed, originated at position slightly posterior the insertion of dorsal fin; with one procurrent ray, and eight rays. Caudal fin moderately forked (deeper than in *P. brachyurus*), with four dorsal procurrent rays, four ventral procurrent rays, and 19 (10+9) principal rays.

Cephalic lateral line well-developed. Supratemporal canal and otic canal not interrupted, each with four pores. Supraorbital canal not interrupted, except the area between the nasal and frontal portions, with 10 pores. Infraorbital canal not interrupted, with 10 pores. Preopercular canal not interrupted, with seven pores. Mandibular canal with three pores. Body lateral line short, the last pored scale about halfway between the posterior margin of pectoral fin and base of pelvic fin; lateral line pored scales often 15. Abdomen anterior to pelvic fin usually scaleless, but some specimens bear scales in posterior portion of region between isthmus and pelvic fin base (Berg 1949).

Pharyngeal bone moderately broad, both the posterior and anterior limbs slightly bent; pitted surface broad, with six major fossae. Pharyngeal teeth in two rows, 5.1-1.5. Teeth slender, hooked at tip in main row; without hooks in minor row.

Vertebrae 37, precaudal vertebrae 21, caudal vertebrae 16.

Intestine short, shorter than standard length, simply looped. Gas bladder short and broad, the anterior chamber almost equal to the posterior one in length, constriction short. Pneumatic duct connecting with the anterior portion of the posterior chamber. Peritoneum slightly brown in color.

Tuberculation. No detailed data about tuberculation of this species are available though the male was hypothesized by Howes (1985) to bear tubercles on breast scales during breeding season. According to Berg (1949), breeding males apparently lack tubercles on the head.

Coloration. A lateral dark stripe present along middle of sides of the body, extending from dorsal end of gill cleft to caudal fin base. Stripe darker posteriorly, darkest on caudal peduncle, and faintest anterior to pectoral fin. Some individuals with a few small dark speckles on sides of body. The mid-dorsal dark stripe extending from nape to caudal fin base. Melanophores present on entire body, except abdomen anterior to anal fin origin and ventral side of the head. Few melanophores present on ventral side of caudal peduncle. All fins bearing melanophores.

Biology

A 45 mm total length female individual was reported to be ripe (Berg 1949). No other data are available at the present time.

Distribution

P. issykkulensis is endemic in Lake Issyk-kul and its tributaries in Kazakhstan (Berg 1949).

Etymology

The epithet *"issykkulensis"* is derived from the combination of "Issykkul" and a Latin suffix "-ensis" to refer the type locality Lake Issyk-kul and its tributary in Central Asia (Kazakhstan) where the species is endemic.

Phoxinus neogaeus Cope, 1868

Synonymy

Chrosomus eos Cope, 1864 – Cope 1864: 281 (non Cope 1861: 523) (mis. ident., comparison with *Phoxinus erythrogaster*, New Hudson, Livingston County, Michigan).

Chrosomus neogaeus (Cope) – Underhill 1957: 12, 25, 30, map 6 (Minnesota); Bailey & Allum 1962: 40, 120, tab.9, fig.3 (desc., dist., South Dakota); New 1962: 147, 149-151, tab.1, figs.1-5 (external morphology); Tyler 1966: 349-361 (physiology); Roberts 1973: 468 (new record, Albert, Canada); Scott & Crossman 1973 : 393, 396-399, figs. p.396, 398 (desc., dist. Canada); Eddy & Underhill 1974 : 240, 241, fig.5 (whole body); Mahy 1975a: 1, 3, 5, 10, 14, 19, 23, 25-29, figs.1-23 (osteology); Mahy 1975b: 165, 168, 172, 175, figs.1-18 (osteology); Mahy 1975c: 617, 619-634, tab.1. figs.1-3, 6, 8-9, 10-22 (osteology); Stasiak 1977: 771-773, tabs.1-4 (morphology and variation, Mississippi River); Gasowska 1979: 373 (name).

Leuciscus neogaeus (Cope) – Fowler 1918: 16-17, pl.6 [desc. (ANSP 4548, cotype of *P. neogaeus*, New Huddson, Livington County, Michigan, and other small and poor preserved 37 specimens)].

Pfrille neogaea (Cope) – Jordan 1924: 71 (change of *Phoxinus neogaeus* to *Pfrille neogaea*); Hubbs & Brown 1929: 27, 28 (tubercles; dist., Superior Lake drainage, Lake Huron drainage, Ontario, Canada); Toner 1933: 137(name); Churchill & Over 1938: 54 (desc., dist., Cox Lake, NW Spearfish, Dakota); Lindeborg 1941: 160 (dist., Ontario, Canada); Hubbs & Lagler 1949: 56, 64, fig.130 (Great Lakes region); Scott 1957: 161 (dist., Lonepine Creek and Loch Leven, Canada); Phillips & Etnier 1969: 96 (name); Eddy & Underhill 1974: 241 (name); Gasowska 1979: 372, 373, 375, 378, 379, 381, 383, 385, 386, 388, 392, 398, 399, figs.3, 10, 17, 23, 29, 37, 42, 48, 69, 67, 75, 79 (osteology); Constantinescu et al. 1984: 286 (name).

Phoxinus neogaeus Cope – Günther 1868: 247 (desc., New Hudson, Michigan); Cope 1869: 375 (original desc.; type locality: New Hudson, Livingston County, Michigan) (in Günther 1868: 247); Jordan 1885: 62 (Wisconsin River, Illinois); Legendre & Steven 1969: 913, tab.I (chromosomes); Legendre 1970a: 325, 329, tabs.1, 2 (vertebrae); Legendre 1970b: 1167-1169, 1171, 1174-1176, tab.I, figs.2, 4, 6, 7 (dist., Quebec, Canada); Gilbert 1971: 476, 477 (name); Mahy 1972: 728 (osteology); Joswiak 1980: 2, 3, 5, 6, 7, 13, 15, 27-22, tabs.2, 4, 5, figs.1B, 2 (chromosome study); Joswiak et al. 1980: 913, tab.1, fig.1B (chromosomes, Wyoming); Stasiak 1980b: 338, fig.on p. 338 (general review); Joswiak, et al. 1982: 968, 969-972, tabs.1, fig.1 (external morphology); Cooper 1983: 112, 114, fig.on p.114 (whole body) (desc., dist., Pennsylvania); Gasowska 1983: 99 (name); Böhlke 1984: 84 (type specimens in ANSP); Constantinescu, Vintilă & Damian 1984: 286, tab.1 (coloration, behavior, and comparison with other *Phoxinus* species); Howes 1985: 71 (name); Coad 1987: 45 (dist., Ottawa, Canada); Dawley et al. 1987: 275-282 (chromosomes); Dawley & Goddard 1988: 649-657, tab. 1 (chromosomes); Harbicht et al. 1988: 475, tab.3, fig.3 (new record, Manitoba, Canada); Starnes & Jenkins 1988: 517 (name); Banarescu 1989: 92, fig.2 (dist. map, North America); Das & Nelson 1989: 579, 583, fig.1A (Albata, Canada); Goddard et al. 1989: 268, 269, 271-277, Appendix, fig.1 (comparison on coloration and behavior among species of *Phoxinus*); Mayden 1989: 260 (name); Goddard & Dawley 1990: 1052-1063, tab.1 (New Hampshire); Nelson & Paetz 1992: 155, 157, 158, fig.on p.155 (whole body), map. 12.9 (dist., Alberta, Canada).

Pfrille neogaeus (Cope) – Jordan et al. 1930:21 (name).

Phoxinus (Pfrille) neogaeus (Cope) – Gasowska 1979: 403 (name).

Material studied

Syntypes: ANSP 5408, 7 alch.; New Hudson, from streams flowing into Lake Erie, Oakland County, Michigan, USA; collector unknown; date unknown.

Other specimens. ANSP 48468, 10 alch.; Otter Pond Camps, Caratunk, Maine; W. J. Epting; 1915. – ANSP 50149, 2 alch.; Bay View, Michigan, USA; T. L. Hankinson; date unknown. – CAS (SU) 09835, 41 alch.; Cross Lake Thoroughfare, Eagle Lakes, Aroostock County, Maine, USA; Kendall and Gould; date unknown. – KU 1146, 3 alch.; Pond in Wilderness Park, Emmet County, Michigan, USA; U.B.S Ichthyology class; 24 July 1946. – KU 1148, 2 alch.; Pond in Wilderness Park, Michigan, USA; Biological Survey; 24 July 1946. – KU 8521, 6 alch. and 3 C&S; Snake River, Cherry County, Nebraska, USA; R. Peckham; 21 August 1963. – KU 14254, 2 alch.; Itasca Park, French Park, Beaver Pond, Clearwater County, Minnesota, USA; R. Stasiak; 1 March 1970. – KU 18882, 3 alch. and 12 C&S; Rennie River, Whiteshell Provincial Park, Manitoba, Canada; F.R. Cook & J.C. Cook; 14 August 1964. – UT 44.1506, 2 alch.; Lena Lake, Lake County, Minnesota, USA; Minnesota Department of Conservation; 1964. – UT 44.2870, 41 alch.; Victor Lake near Midiwan Lake, 5 mi. N.W. Isabella, Cook County, Minnesota, USA; D.A. & M.A. Etnier, L.B. & W.C. Starnes; 21 June 1982. – UT 44.2894, 14 alch.; Hill Creek tributary to Midiwan Lake at logging road and above in beaver pond, Kauishiwi system, Cook County, Minnesota, USA; D.A. & M.A. Etnier, W.C. & L.B. Starnes; 21 June 1982.

Diagnosis (amended from Cope 1869)

A *Phoxinus* with one narrow lateral dark stripe almost equal in width from anterior to posterior portion of body; the lateral stripes are continuous onto head and across snout. Mouth large, its opening extending to below anterior margin of pupil of eye. In spawning males, first five (occasionally four) pectoral rays much darker, thicker and stronger than other pectoral rays; segments of these thick rays short and wide. Intestine short with only one loop, its length less than standard length; pneumatic duct dark; pharyngeal teeth in two rows, 2.5-5.2, 2.4-5.1, or 1.5-4.1; pharyngobranchial 4 bearing a median process.

Description (Tab.5)

A North American species of *Phoxinus* with average standard length (adults) about 70 mm. Head large, broad, and robust, its length 27% of standard length, its width 58% of its length. Snout short and blunt; its length 26% of head length, 93% of orbit length. Eye lateral on head and large; orbit length 28% of head length. Mouth large (largest in *Phoxinus*), terminal, and oblique, its opening extending below the anterior margin of eye pupil. Lower jaw slightly shorter than the upper one.

Tab.5: Body proporations (%) of *Phoxinus neogaeus*. (ACGL: anterior chamber of gas bladder length; BD: body depth; BIW: bony interorbital width; CPD: caudal peduncle depth; CPL: caudal peduncle length; HD: head depth; HL: head length; HW: head width; IL: intestine length; Number: number of specimens; OL: orbit length; PCGL: posterior chamber of gas bladder length; PRDL: predorsal fin length; PRPL: prepelvic fin length; S: standard deviation; SL: standard length; SNL: snout length).

	HL/SL	HD/SL	BD/SL	CPL/SL	CPD/SL	PRDL/SL	PRPL/SL	IL/SL	HW/SL	HD/HL
Number	17	18	17	18	18	17	16	3	18	17
	26.0	16.4	18.8	21.5	9.0	54.7	49.1	77. 0	14.1	58.6
Range	–	–	–	–	–	–	–	–	–	–
	30.2	22.1	23.5	34.2	27.3	61.6	65.7	85 .1	17.3	75.0
Mean	27.4	18.3	21.6	25.2	11.5	57.4	50 .1	81.0	16.0	66.1
S(±)	1.4	1.8	1.5	2.8	4.0	2.0	8.3	4.1	1.1	4.5

	OL/HL	HW/HL	SNL/HL	BIW/HL	BIW/OL	SNL/OL	PRDL/ PRPL	CPD/CPL	ACGL/ PCGL
Number	17	16	17	17	17	17	14	17	3
	23.1	52.4	22.5	29.7	82.2	68.6	107.8	2 6.4	38.5
Range	–	–	–	–	–	–	–	–	–
	33.7	65.7	29.2	43.5	142.9	100.0	117.1	52.0	75.0
Mean	28.2	58.2	25.9	33.9	116.6	92.9	1 12.8	43.2	54.5
S(±)	3.4	3.5	2.0	3.2	19.5	10.3	3.0	6.2	18.7

Bony interorbital space wide; its width 117% of orbit length, and 34% of head length.

In young individuals (25 mm standard length), axis of olfactory organ short, not extending to middle of the organ, five primary lamellae present; in adult individuals (52.0 mm standard length), axis extends to posterior portion of the organ, 11 primary lamellae present.

Body not strongly compressed. Its maximum depth 22% of standard length. Caudal peduncle short and high, its length 25% of standard length, its depth 43% of its length.

Genital papillae short and small; longer and more slender in female than in male; its posterior end far forward of anal fin origin.

Pectoral fin fan-like, sharper in female. In breeding male, first four or five rays, especially the first one, thicker, stronger, and darker than rest of pectoral rays; segments of these thick rays shorter and wider; 13-16 fin-rays, usually 14 or 15. Pelvic fin originating in advance of dorsal fin origin, prepelvic length 50% of standard length; fin rays eight, occasionally nine (two of the 17 specimens counted with nine rays).

Dorsal fin originating posterior to pelvic fin origin, predorsal length 57% of standard length, and 113% of prepelvic length; with two procurrent rays and eight rays, only one of the 18 specimens with nine rays. Anal fin originating under or slightly behind the insertion of dorsal fin; with one or two procurrent rays and eight fin rays. Caudal fin shallowly forked, lobes round; with 7-9 dorsal procurrent rays, 5-7 ventral procurrent rays and 19 (10+9) principal rays.

Left and right supratemporal canals not connecting with each other; six pores. Otic canal with six pores. Supraorbital canal interrupted in some specimens, 12 pores. Infraorbital canal without interruption, 14 pores. Preopercular canal extending to middle of the preopercle, 10 pores. Mandibular canal without interruption, 6 pores.

Body lateral line extending from dorsal of gill cover, curving down and following lateral stripe, and ending at the level of the pelvic fin; with about 31 pored scales, depending on specimen's size. (Large individuals have more pored scales than juveniles.) Scales well embedded, covering entire body.

Pharyngeal bone somewhat slender; posterior limb straight; pitted surface narrow with four to five major fossae. Pharyngeal teeth in two rows, 2.5-4.2, 2.4-5.2, 2.5-5.2, or 1.5-4.1. Teeth robust, hooked at tip (not hooked for one or two teeth near posterior limb). Masticatory surface of teeth smooth.

37 or 38 vertebrae; 21-22 precaudal vertebrae, 15-17 postcaudal vertebrae.

Intestine short and simply coiled, its length 81% of standard length. Anterior chamber of gas bladder shorter than posterior one; the younger the individual, the more similar the two chambers in length. For instance, anterior chamber length 75% of posterior one's length in a 43.5 mm standard length individual, and 50% of the posterior length in a 60.6 mm standard length individual. Pneumatic duct placed at constriction of gas bladder. Peritoneum dark.

Tuberculation. Tubercles present on entire body (lateral, dorsal, and ventral sides of body; and dorsal and lateral sides of head). Each scale in seven or eight rows on breast bearing three to five tubercles at the apical margins. Ventral side of body with fewer tubercles than sides and dorsum. Each anterolateral scale bearing one or two rows of tubercles; one row close to apical margin, consisting of 4-6 tubercles; second row remote from the margin consisting of 1-3 tubercles. Each scale on the caudal peduncle bearing about 6 tubercles on its apical margin. Tuberculation on fins similar to that in *P. cumberlandensis* (see below).

Coloration. A distinct lateral black stripe extending from anterior end of snout to caudal fin base, ending in a distinct round black spot at caudal base. Stripe uniformly narrow through its length. The mid-dorsal dark stripe extending from the nape to base of caudal fin, best developed pre-dorsally.

In some specimens, very few melanophores are evident below the lateral stripe and ventral side of body (including chin), except for a small area near base of pectoral fin. In other specimens, melanophores are present on entire body. Melanophores are concentrated along ventral edge of caudal peduncle, forming an elongated dark area on this region.

All fins bearing numerous melanophores. On dorsal, anal, pelvic and pectoral fins, melanophores almost evenly distributed though the anterior rays have slightly more melanophores than the posterior rays in all fins. In breeding males, however, first four or five thick rays of pectoral fin bear more melanophores than the rest, so these thick rays look very dark, the other rays almost colorless.

Biology

The biology of *Phoxinus neogaeus* is poorly known. Scott & Crossman (1973) summarized the general biology of the species in Canada. Stasiak (1978) studied reproductive biology in Minnesota. Other data are reported by Hoffman (1967) (parasites), Tyler (1966) (temperature tolerance), and Constantinescu et al. (1984) (behavior).

This minnow prefers cool bog ponds, streams, and small boggy creeks and lakes. Fish species associated include *Phoxinus eos, Pimephales promelas, Umbra limi, Culaea inconstans* in Minnesota (Stasiak 1978); *Phoxinus eos, Margariscus margarita*, and *Culaea inconstans* in Canada (Scott & Crossman 1973). Hybrids, *P. neogaeus x eos,* are frequently found at some localities (Hubbs & Brown 1929, New 1962, Legendre 1970b, Stasiak 1978, Joswiak et al. 1982, Joswiak et al. 1985, Das & Nelson 1989, Goddard & Dawley 1990).

Few data about food of this species are available. Scott & Crossman (1973) examined a few specimens and found that the summer diet of this species was composed mainly of insects, though some crustaceans and plankton were present. Protozoan parasites were observed in the species' diet, such as *Myxosoma parellipticoides* (Hoffman 1967).

The spawning season begins in late April, reaches its peak in early May, and concludes by end of May in Minnesota (Stasiak 1978). It is later in Canada. Spawning probably occurs in June in northern Ontario (Scott & Crossman 1973). Breeding behavior of *Phoxinus neogaeus* seems complicated: females and males leave a large school, then males stimulate females with pectoral fin placed under belly of females, and with tubercles rubbing against ventral side of the female. Fecundity of this minnow was estimated from 784 to 3060 eggs (Stasiak 1978).

Growth pattern (relationship between length and age) of both sexes was similar when fish were young (≤ 1 year). Females grow faster than males thereafter and have longer life spine. Six-year-old females and five-year-old males have been found (Stasiak 1978).

Distribution

This is one of the northernmost distributed species of *Phoxinus* in North America. It occurs widely in bog ponds, streams and lakes from the Arctic circle in Mackenzie River drainage (Canada) in northwest to St. Lawrence and Atlantic drainage (including New Brunswick, Maine, and New Hampshire) in the east, and Southern Quebec, northern New York State, north of lower Great Lakes to Michigan in the south (Scott & Crossman 1973, Stasiak 1980b). Isolated populations were found in South Dakota (Evermann & Cox 1896, Churchill & Over 1933), Nebraska, Colorado & Wyoming (Bailey & Allum 1962). Scott & Crossman (1973) and Stasiak (1980b) provided maps of the geographic distribution of this species in Canada and North America, respectively.

Comments

The genus name used for this species has had an interesting cycle history. It was originally described by Cope (in Günther 1868) as *Phoxinus neogaeus*. Fowler (1918) called it to *Leuciscus neogaeus*. Jordan (1924) proposed a new genus, *Pfrilles* with *Phoxinus neogaeus* as the type species. No ichthyologists considered it as a species of the *Chrosomus* to which *P. erythrogaster* belonged until Bailey (1951). Although Hubbs and Brown (1929) discussed a close relationship between *Phoxinus* (*P. phoxinus* and *P. neogaeus*) and *Chrosomus*, Bailey (1951) first merged *P. neogaeus* and other North American *Phoxinus* species into the single genus *Chrosomus*. Banarescu (1964) considered *Chrosomus* a synonym of *Phoxinus*. Thus, through a long way of change, this minnow returned to its original genus *Phoxinus*. After Banarescu (1964), some ichthyologists used the name *Phoxinus neogaeus* (e.g., Mahy 1975c), others used *Pfrille neogaea* (e.g. Gasowska 1979), or *Chrosomus neogaeus* (e.g., Stasiak 1977) for this species. Most ichthyologists seem to agree to use name *Phoxinus neogaeus* for this dace since the early 1980s (e.g., Stasiak 1980). Because hybrids of *P. neogaeus* and *eos* have been found from many places, and hybrids are fertile (Legendre 1970b), some ichthyologists considered these two species sharing a close relationship (e.g., Scott & Crossman 1973), which is not supported by this publication.

Etymology

The epithet name of this species "*neogaeus*" means "new-world" (for neo- and -gaeus) (Nelson & Paetz 1992), referring the species as a New World species of *Phoxinus*.

Phoxinus cumberlandensis Starnes & Starnes, 1978

Synonymy

Chrosomus erythrogaster Rafinesque, 1820 – Jordan & Swain 1883: 248 (mis.id., based on color desc., Whitley County, Kentucky).

Phoxinus cumberlandensis Starnes & Starnes, 1978 – Starnes & Starnes 1978: 508, 509, 512, 513-515, tabs. 1-2, figs.1, 2A, 3A, 4 (orig. desc., Type locality: Cumberland River drainage of Kentucky and Tennessee); Joswiak et al. 1980: 914, tab.1, fig.1A (Chromosomes, Kentucky); Starnes & Starnes 1980a: 335, fig. p.335 (no figure number) (general review); Starnes & Starnes 1981: 360-362, 364-370, tab.1, figs.1-3 (biology, Upper Cumberland River); Warren 1981: 129, 132-133 (new record, eastern Kentucky); Böhlke 1984: 74 (type specimens in ANSP); Constantinescu et al. 1984: tab.1 (coloration and behavior comparison with other *Phoxinus* species); Starnes & Jenkins 1988: 517, 521, 526 (name); O'Bara 1990: 9, 10, 12, 13, tabs.1, 2 (new record and ecology, Upper Cumberland River); O'Bara 1991: (no page number, ecology and behavior).

Phoxinus sp. 1977 Starnes & Starnes 1977: 1-3, figs.1-3 (dist. and population status, Upper Cumberland River).

Material studied

Paratypes: ANSP 138365, 13 alch.; Eagle Creek at Kentucky 896, 3.4 km NE of Kentucky, 90 jct., McCreary County, Kentucky, USA; W.C. & L.B. Starnes; 29 May 1977. – USNM 217810, 85 alch.; Younas Creek at Gravel Road, 0.8 km west of US 25W, 10.7 Air km N W of Williamsburg, Whitley County, Kentucky, USA; W.C. Starnes & L.B. Starnes; 6 September 1976. – UT 44.1366, 5 alch.; Lawson Branch (tributary to Capuchin Creek) at gravel road 4.8 km SSW of Scott-Campbell-McCreary County line corner, Scott County, Tennessee, USA; W.C. & L.B. Starnes; 7 May 1977.

Other materials: KU 18934, 8 C&S; Youngs Creek, Whitley County, Kentucky, USA; W.C. Starnes & L.B. Starnes; 25 September 1977. – UT 44.3390, 3 alch.; Davis Branch, tributary to Little Yellow Creek, near US 25E, Cumberland Gap State Park, Bell County, Kentucky, USA; W.L. Pennington & J.R. Shute; 18 November, and 10 December 1985. – UT 44.3905, 3 alch.; Baird and Hatfield Creeks, Cambell County, Tennessee, USA; WAPORA, Inc., project 524; 7 March 1981. – UT 44.4000, 1 alch.; Long Branch, River mile 0.5, Bell County, Kentucky, USA; O'Bara and Swan; 8 November or 11 August 1984. – UT 44.4001, 8 alch.; Young's Creek, County road 204, Whitley County, Kentucky, USA; O'Bara and Swann; 9 October or 10 September 1984. – UT 44.4519, 1 alch.; Straight Creek, 2.9 rd mi. from Tenn. 90 on straight Creek Road, Claiborne County, Tennessee, USA; D.A., E.A., & M.A. Etnier, SE McLain, WW EVE; 23 April 1989.

Diagnosis (amended from Starnes & Starnes 1978)

A *Phoxinus* with one single wide black lateral stripe (two stripes in young) extending from anterior of nasal opening to the caudal fin base; no connection between the left and right stripes at anterior of snout; intestine elongate with six loops in adults; opercle elongated and narrow; epibranchials 2 and 4 bearing an elongate posterior process; epibranchial 5 with a deep broad concavity on its posterior margin; pharyngeal bone with a notch at its posterior limb; anterior process of basioccipital elongate; often displaying a head-down swimming attitude (Starnes & Starnes 1978).

Description (Tab.6)

A North American species of *Phoxinus* reaching about 60 mm standard length. Head short, its length 25% of standard length, its width 51% of its length. Snout short and blunt, its length 17% of head length, 101% of orbit length. Eye lateral on head, moderately large; orbit length 29% of the head length. Mouth small and slightly oblique; its gape not extending to below anterior margin of eye. Lower jaw shorter than upper one, and included by the latter.

Bony interorbital space wide, its length 101% of orbit length, and 32% of head length.

In young individuals (SL ≤23.5 mm), axis of olfactory organ semi-round and located in anterior portion of organ, four primary lamellae placed around posterior margin of axis. In adults, axis elongate and located mesially extending from anterior to posterior parts of organ; ten primary lamellae present along lateral and mesial margin of axis. Melanophores present on primary lamellae and axis in most specimens.

Body moderately deep and slightly compressed. Maximum body depth 25% of standard length. Caudal peduncle high and relatively short, its depth 35% of its length.

Pectoral fin with 13-18 rays, 15 rays in most specimens. Pectoral fin round, its distal tip close to origin of pelvic fin in male; pectoral fin sharper, shorter, and not approaching to origin of the base of the pelvic fin in females. Pelvic fin with 7-9 rays, eight rays in most specimens; prepelvic length 47% of standard length.

Tab.6: Body proportions (%) of *Phoxinus cumberlandensis*. (ACGL: anterior chamber of gas bladder length; BD: body depth; BIW: bony interorbital width; CPD: caudal peduncle depth; CPL: caudal peduncle length; HD: head depth; HL: head length; HW: head width; IL: intestine length; Number: number of specimens; OL: orbit length; PCGL: posterior chamber of gas bladder length; PRDL: predorsal fin length; PRPL: prepelvic fin length; S: standard deviation; SL: standard length; SNL: snout length).

	HL/SL	HD/SL	BD/SL	CPL/SL	CPD/SL	PRDL/SL	PRPL/SL	IL/SL	HW/SL	HD/HL
Number	33	35	5	33	33	34	32	2	3 5	33
	24.0	12.0	24.0	22.2	22.0	50.0	39.0	14 2.9	12.0	50.4
Range	–	–	–	–	–	–	–	–	–	–
	30.0	17.0	26.5	29.1	29.0	63.0	50.0	31 8.9	16.0	63.5
Mean	25.0	15.0	25.2	26.0	26.0	54.0	47 .0	230.9	13.0	58.9
S(±)	1.0	1.0	2.0	1.9	2.0	3.0	2.0	124.5	1.0	3.3

	OL/HL	HW/HL	SNL/HL	BIW/HL	BIW/OL	SNL/OL	PRDL/ PRPL	CPD/CPL	ACGL/ PCGL
Number	31	33	33	33	34	34	34	31	4
	22.1	45.8	14.0	28.0	74.2	76.2	92.9	29.5	55.0
Range	–	–	–	–	–	–	–	–	–
	35.3	56.3	20.8	38.0	116.7	133.3	122.3	43.0	70.0
Mean	29.1	50.6	17.2	32.0	100.9	101.0	113.7	34.6	60.4
S(±)	3.3	3.6	1.8	3.0	1.64	16.5	7.6	4.6	6.7

Dorsal fin originating above base of pelvic fin, ending above anal fin origin; predorsal length 54% of standard length, and 114% of prepelvic length; with one or two procurrent rays, eight rays. Anal fin small, with one procurrent ray, seven or eight fin rays. Anal fin longer in females than in males. Caudal fin deeply forked, lobes nearly acute, with eight or nine dorsal procurrent rays, seven or eight ventral procurrent rays, and 19 (10+9) principal rays.

Scales small, especially on belly. Scales poorly-embedded or well embedded on sides, deeply embedded ventrally. Scales on the caudal peduncle less embedded than that the remaining body.

No cephalic line pore present in individuals less than 25 mm standard length. Left and right supratemporal canals short and far from each other, with six pores. Supraorbital canal broadly interrupted at different points, with 10 pores. Otic canal with five pores. Infraorbital canal with 13 pores. The preopercular canal with 12 pores. Mandibular canal with four pores.

Body lateral line varying from absent in young to complete in adults. Body lateral line straight in adults and extending from posterior of the opercle to base of the caudal fin. Lateral line interrupted in different places. Pored scales about 62.

Pharyngeal bone developed, pitted surface flat and wide. Pharyngeal teeth in one row, 5-5, occasionally 4-5, or 5-4. Teeth thin, elongate, and hooked at tip.

Vertebrae 37-39; precaudal vertebrae 20-21, caudal vertebrae 17-19.

Intestine long with complex loops, six loops in adults. Relative length of intestine increases as the fish grows, its length about 230% of standard length in adults. Gas bladder short and broad. Anterior chamber broad and round anteriorly, its posterior portion not much narrower than anterior portion; anterior chamber 60% of posterior chamber in length. Constriction elongated, pneumatic duct connecting with middle portion of constriction. Peritoneum dark in color.

Tuberculation. Dorsal, lateral and ventral sides of head bearing scattered small tubercles. Each breast scale bearing 4-5 tubercles at its apical margin (up to 12 on some scales). Each scale on the anterolateral body bearing 2-5 tubercles in one row located near the apical margin of the scale in most specimens; tubercles in two rows in a few specimens. Scales on upper part of the body sides (dorsal to lateral line) bearing better developed tubercles than scales on lower part of sides (ventral to lateral line). Tubercles on apical margin of caudal peduncle scale. Second to fifth pectoral fin rays bearing two rows of tubercles per ray on the dorsal side of the fin, the membrane between the rays also bearing a few tubercles; other fin rays and membrane on the dorsal side, and all rays and membranes on the ventral side, bearing fewer and smaller tubercles. Each pelvic ray bearing one row of tubercles dorsally, and a few tubercles ventrally. Tubercles on dorsal and anal fins small and uniserial. Tubercles absent on caudal fin.

Coloration. The most characteristic color pattern is a broad dark lateral stripe, extending from in front of anterior nasal opening to base of caudal fin. The left and the right lateral stripes are not connecting each other at the end of the snout. Young with two dark stripes that converge into one on the caudal peduncle. Females bearing less developed stripe than males. Body lateral line extends within the stripe. Numerous small black speckles randomly present dorsal to the stripe and on dorsum of body and head. Melanophores absent dorsally on tip of snout. Mid-dorsal stripe present, interrupted once or twice in the predorsal fin region, and the postdorsal fin region. No melanophores present ventral to lateral stripe and silver in color at ventrolateral sides of body and ventral side of head. A few melanophores present on some pectoral and anal rays, and all dorsal and caudal rays. Base of dorsal fin densely pigmented. Caudal fin darker than other fins. The coloration in life was described by Starnes & Starnes (1978).

Biology

The biology of *P. cumberlandensis* was studied by Starnes & Starnes (1978, 1981) and O'Bara (1990, 1991). The following information is abstracted and summarized from those publications.

P. cumberlandensis is restricted to small streams with cold and clear water. In Young's Creek of Kentucky where the dace was found, the water temperature is generally below 23°C. The dace also requires a ratio of riffle area to pool area 60:40 or below. Fish species associated with the *P. cumberlandensis* include *Semotilus atromaculatus, Rhinichthys atratulus, Campostoma anomalum, Pimephales notatus, Catostomus commerso-*

ni, Etheostoma kennicotti, Etheostoma sagitta, and occasionally *Phoxinus erythrogaster*. Diet of *P. cumberlandensis* varies, mainly including sand (35%), algae (8.4%), invertebrates (4.6%), and some other unidentified organic materials (32.1%). Its diet differs from that of most sympatric species in that invertebrates occupy a very small portion of the whole diet (4.6%); whereas, in other species invertebrates comprise from about 50% (e.g., *Catostomus commersoni*), to almost 100% (e.g., *Etheostoma sagitta*, and *E. kennicotti*). However, its diet is similar to that of *Campostoma anomalum, Pimephales notatus*, and *Phoxinus erythrogaster*.

This dace spawns on nest of stoneroller, *Campostoma anomalum*. Its average fecundity is 1540 ova per female. *P. cumberlandensis* grows rapidly the first year, more slowly in the second and third years. Starnes & Starnes (1981) estimated the standard length of the species at the end of the first year as 35.4 mm, end of the second 54.3 mm, and the end of the third 65.5 mm for the dace from the Young's Creek in Kentucky. The life span of the fish was estimated to be 3 years.

Distribution

P. cumberlandensis is restricted to small streams of the upper Cumberland River basin in Kentucky and Tennessee, USA (Starnes & Starnes 1978). It has been found in 30 streams of the Cumberland River drainage (O'Bara 1990).

Comments

Starnes & Starnes (1978) considered *P. cumberlandensis* more closely related to *P. oreas* than to any other *Phoxinus* species, because these two species share similar-shaped opercle, long and complicated looped intestine, and nuptial coloration. Because of its restricted and isolated distribution, and habitat degradation resulting from human activities, mainly from coal mining, this dace is currently listed as a threatened species by the U.S. Fish and Wildlife Service. O'Bara (1990) reported it was apparent absent from eight creeks where it was found from 1979 to 1981.

Etymology

The epithet *"cumberlandensis"* derives from a combination of "Cumberland" and Latin suffix "-ensis" referring to the Cumberland River drainage where the species is endemic (Starnes & Starnes 1978).

Phoxinus tennesseensis Starnes & Jenkins, 1988

Synonymy

Chrosomus erythrogaster (Rafinesque) – Henshall 1889: 31 (Whiteside, Tennessee, mis. id.); Evermann & Hildebrand 1916: 443 (Roariny Fork, Tennessee, mis. id.); Evermann 1918: 339 (mis. id.); Fowler 1923: 9 (Holston, Vagiania, mis. id.); Fowler 1924: 391 (Holston, Vagiania, mis. id.); Fowler 1936: 111 (Hiwassee System, Tennessee, mis. id.).

Chrosomus oreas ssp. – Ross and Carico 1963: 12 (Pigeon System, Tennessee); Jenkins, Lachner & Schwartz 1972: 48, 98 (Tennessee River drainage); Stauffer et al. 1982: 35 (Tennessee River drainage); Starnes & Etnier 1986: 347 (Tennessee River drainage).

Leuciscus erythrogaster (Rafinesque) – Cope 1868: 241, 245, 247 (Middle Fork, Holston System, Vafiania, mis. id).

Phoxinus erythrogaster (Rafinesque) – Hitch & Etnier 1974: 84 (Hiwassee System, Tennessee, mis. id.).

Phoxinus sp. – Hitch & Etnier 1974: 84 (Hiwassee System, Tennessee).

Phoxinus tennesseensis Starnes & Jenkins, 1988 – Starnes & Jenkins 1988: 517, 519, 523-527, tab.1, figs.1 a-c, 2b, 3 (orig. desc.; type locality: Little River System, Blount County, Tennessee); Schilling & Ryon 1993: 274 (reproductive biology, Tennessee).

Material studied

Paratypes: UT 44.992, 7 alch.; Tributary to Bear Creek at Tenn. 95, Andersoa County, Tennessee, USA; D.A. Etnier, W.C. Starnes, G.A. Schuster, W. Scraw, J. Lowa, & Adams; 1 December 1974. – ANSP 134735, 12 alch.; Clinch River system, tributary to east fork Polar Creek at Tenn. 95, 6.2 road mi. N of Clinch River, Roane County, Tennessee, USA; W.C. Starnes & L.B. Starnes; 15 February 1975. – USNM 216212, 15 alch.; Holston River system, Surgoinsville Creek, 1.2 road mi. north of US 11w (Surgoinsville), Hawkins County, Tennessee, USA; W.C. Starnes et al.; 30 November 1975.

Other Materials: UT 44.575, 2 alch.; Chestuee Creek at Nonaburg, McMinn county, Tennessee, USA; R. & S. Hitch; 25 October 1970. – UT 44.98, 2 alch.; Caney Branch, Citico Creek drainage, Nonroe County, Tennessee, USA; R. Tatum & J. Elier; 16 January 1967. – UT 44.5274, 4 alch.. and 2 C&S; Ocoee river system, Polk County, Tennessee, USA; W.L. Pennington et al.; 25 February 1991. – ANSP 22112, 2 alch.; South Fork, Holston River, Virginia, USA; E.D. Cope; date unknown.

Diagnosis (amended from Starnes & Jenkins 1988)

A *Phoxinus* with two lateral dark stripes, the lower one interrupted into two sections; elongate and complex coiled intestine; pneumatic duct connecting with posterior chamber of gas bladder; anterior margin of anterior ceratohyal concave; medial ramus of tripus robust and broad.

Description (Tab.7)

A North American species of *Phoxinus* with maximum standard length of 60 mm. Head large, broad, and robust, its length 25%, its width 61% of standard length. Snout short, its length 27% of head length, 100% of orbit length. Eye lateral on head, moderately large; orbit diameter 30% of head length. Mouth small, subterminal and oblique, its gape not extending below anterior margin of eye. Lower jaw shorter than upper one.

Bony interorbital space wide, its width 112% of orbit length, and 33% of head length. Anterior nasal opening larger than posterior one. Entire margin on anterior nasal opening erect. Posterior, lateral and mesial portions of posterior nasal opening's margin not erect.

Tab.7: Body proportions (%) of *Phoxinus tennesseensis*. (ACGL: anterior chamber of gas bladder length; BD: body depth; BIW: bony interorbital width; CPD: caudal peduncle depth; CPL: caudal peduncle length; HD: head depth; HL: head length; HW: head width; IL: intestine length; Number: number of specimens; OL: orbit length; PCGL: posterior chamber of gas bladder length; PRDL: predorsal fin length; PRPL: prepelvic fin length; S: standard deviation; SL: standard length; SNL: snout length).

	HL/SL	HD/SL	BD/SL	CPL/SL	CPD/SL	PRDL/SL	PRPL/SL	IL/SL	HW/SL	HD/HL
Number	16	16	16	16	16	15	15	3	16	16
Range	22.5 – 26.7	13.7 – 17.1	17.5 – 24.1	22.5 – 27.2	8.0 – 11.5	51.6 – 56.2	43.3 – 50.7	210 .0 – 22 0.4	11.7 – 13.7	55.2 – 63.2
Mean	25.3	15.5	20.4	26.1	9.6	54.2	47. 9	215.2	13.0	61.3
S(±)	1.2	1.1	2.4	1.5	1.1	1.5	2.2	5.2	0.6	4.0

	OL/HL	HW/HL	SNL/HL	BIW/HL	BIW/OL	SNL/OL	PRDL/ PRPL	CPD/CPL	ACGL/ PCGL
Number	16	16	16	16	16	14	14	16	2
Range	26.7 – 40.0	50.5 – 55.1	18.3 – 33.3	28.4 – 36.8	84.4 – 122.9	74.1 – 115.6	109.0 – 123.2	2 9.5 – 44.8	58.0 – 62.0
Mean	29.5	51.5	27.3	32.5	111.9	100.3	114.0	37.1	60.0
S(±)	4.9	2.9	4.4	4.4	16.5	13.2	5.7	5.6	2.83

Morphology of olfactory organ changing less ontogenetically than in other *Phoxinus* species. Young individuals (25.6 mm or less standard length) with an elongate axis situated at middle portion of organ, and extending posteriorly; seven or eight primary lamellae present, without melanophores. Large specimens with axis similar to that in young, with about 11 primary lamellae, melanophores present in most primary lamellae, fewer melanophores present on axis.

Body stout, not strongly compressed, though its posterior part more compressed than the anterior part of body. Maximum depth 20% of standard length. Caudal peduncle length 26% of standard length, its depth 37% of its length.

Genital papilla slender and longer in female than in male; its posterior end close to origin of anal fin. Papilla bearing a skin fold, margin of genital orifice serrated in male, but not in female. Both male and female bearing a short process at posterior end of papilla, the process longer and sharper in male than in female.

Pectoral fin fan-like, sharp and elongate, with 15-17 rays. Pelvic fin originating in advance of dorsal fin origin; pelvic fins sharper and longer in female than in male, the posterior tip extending beyond anal fin's origin in female; posterior margin extending to (not beyond) anal origin in male; with eight rays.

Dorsal fin originates farther posteriorly than origin of pelvic fin; predorsal length 54% of standard length, and 114% of prepelvic length; with three procurrent fin rays, eight fin rays. Anal fin originated slightly behind insertion of dorsal fin; with two procurrent rays, and eight rays. Caudal fin deeply forked, lobes sharp, with 4-8 dorsal procurrent rays, four or five ventral procurrent rays, and 19 (10+9) principal rays.

Scales well embedded, covering entire body. Scales at ventral part of body deeply embedded.

Left and right supratemporal canals widely separated from each other; five pores. Otic canal with eight pores. Supraorbital canal with 10 pores. Infraorbital canal with 15 pores. Preopercular canal with eight pores. Mandibular canal with three pores. Body lateral line pored scales 34, last pored scale located at the position of the posterior margin of the pectoral fin; no pored scales found in individuals smaller than 33 mm standard length.

Pharyngeal bone broad, its posterior limb straight; pitted surface broad with four to six major fossae. Pharyngeal teeth in one row, 5-5. Teeth elongate, slender, and hooked at tip (not or very slightly hooked in one or two teeth near the posterior limb).

Vertebrae 38 or 39; precaudal vertebrae 20, caudal vertebrae 18 or 19.

Intestine long, about six complex loops. Its length 215% of standard length.

Anterior chamber of gas bladder shorter than the elliptical posterior one. Former about 60% of the latter in length. Constriction of the gas bladder developed and elongated. Pneumatic duct connected with anterior portion of the posterior chamber. Peritoneum dark.

Tuberculation. Tubercles present on entire body and head, including their lateral, dorsal, and ventral sides. Dorsal part of snout more densely tuberculated than rest of head. Ventral side of head bearing fewer tubercles than rest of head. Each scale in five or six rows on the breast bearing four or five tubercles on its apical margin. Each scale on anterolateral side of body bearing one tubercle near the apical margin. Scales on posterolateral part of body, especially ventral part of the caudal peduncle, bearing four to six tubercles at apical margin; tubercles in this region more developed than that in other parts of body. Tuberculation on all fins similar to that in *Phoxinus cumberlandensis*.

Coloration. Two lateral stripes present at the sides of body. Lower stripe extending from anterior portion of snout to caudal fin base. In large individuals, lower stripe interrupted at a point dorsal to anal fin origin. In small individuals (less than 30 mm in standard length), the stripe is complete. A dark dorsal stripe extending from nape to caudal fin base without interruption; dorsal stripe more distinct in small individuals than in larger ones.

Numerous melanophores present on sides of body. Region dorsal to the upper lateral stripe darker than region ventral to stripe. Ventral part of body lacking melanophores, except at anal fin base, ventral caudal peduncle and pectoral fin base where few melanophores present. Dorsum and dorsolateral portion of head bearing numerous melanophores. Numerous spots present on area dorsal to the upper lateral stripe in some large individuals, especially in breeding males. Melanophores present on ventral aspect of head. Ventral side of head darker in breeding male than that in breeding female.

Biology

P. tennesseensis occurs in small rivers with fast current and low water temperature (seldom exceeding 20°C), as well as in sluggish ponds with fine gravel, sand and silt substrate. The fish species found associated with *P. tennesseensis* include *Campostoma anomalum* and *Semotilus atromaculatus* (Starnes & Jenkins 1988, Schilling & Ryon 1993).

Diet is not well known. The intestine of some contained mainly organic detritus, algae, and diatoms. Starnes & Jenkins (1988) estimated that diet of the species might be similar to that of *P. oreas* and *cumberlandensis* because of the similarity of the intestine in these three species.

P. tennesseensis may spawn over the nest of gravel-nest-building cyprinids, such as *Campostoma* and *Semotilus* which are normally found with this dace and generally in aggregations of eight to more than 100 individuals. The spawning season occurs from late April to middle June (Schilling & Ryon 1993).

Distribution

P. tennesseensis is restricted to small streams of the Upper Tennessee River drainage in Virginia and Tennessee (Starnes & Jenkins 1988; Schilling & Ryon 1993). Starnes & Jenkins (1988: fig.3) mapped the localities where the dace had been found.

Etymology

The epithet *"tennesseensis"* is a combination of Tennessee and the Latin suffix "-ensis" in reference to the type locality and endemism in the Tennessee River drainage (Starnes & Jenkins 1988).

Phoxinus oreas (Cope, 1868)

Synonymy

Chrosomus oreas Cope, 1868 – Cope 1868: 233, 234, pl 23, fig.7 (orig. desc.; type locality; head of Roanoke River, Montgomery County, Virginia); Jordan 1877: 71 (name); Fowler 1924: 391 (desc.); Hubbs & Brown 1929: 28 (tuberculation); Wiley & Collette 1970: 168 (name); Mahy 1975c: 618-634, tab.1, figs.1-3, 6, 8-12, 14-21 (osteology); Goswaska 1979: 373, 374, 379, 381, 383, 392, 399, 403, figs.6, 24, 32, 33, 39, 44, 50, 55, 62, 69, 82, 88 (osteology); Böhlke 1984: 85 (type specimens in ANSP).

Parchrosomus oreas (Cope) – Gasowska 1979: 404 (osteology and taxonomy).

Phoxinus erythrogaster oreas (Cope) – Mahy 1972: 729 (name); Mahy 1975c: 618, 640, fig.22 (osteology, taxonomy).

Phoxinus oreas (Cope) – Mahy 1972: 728 (name); Stauffer et al. 1975: 123, tab. 1 (dist., East River, West Virginia); Mahy 1975c: 617 (name); Hambrick 1977: 238-242, tab.1, fig.1 (Roanoke River, Virginia); Starnes & Starnes 1978 : 509, 513, 514, figs.2B, C (comparison with *Phoxinus cumberlandensis*); Joswiak 1980: 2, 3, 6, 7, 15, 17, 22, tabs 1, 2, 4, 5 , figs.1C, 2 (chromosome study); Joswiak et al. 1980: 914, tab.1, fig.1C (chromosome study, Virginia); Starnes & Starnes 1980c: 339, fig. on p. 339 (general review); Matthews & Styron 1981: 149, 150, 153, 155, tabs.1, 2, 3 (Physiology, Roanoke River, Virginia); Starnes & Starnes 1981: 362, 367 (name); Böhlke 1984: 85 (name); Starnes & Etnier 1986: tab.10.1 (dist., Tennessee River); Starnes & Jenkins 1988: 517, 519, 523-528, tab.1, fig.2a (comparison with *P. tennesseensis*); Mayden 1991: 260 (name).

Material studied

Paralectotypes: ANSP 4552. 14 alch.; Mountain streams forming the head of the Roanoke River, Montgomery County, Virginia, USA; E.D. Cope; August 1867.

Other materials: ANSP 46543, 18 alch.: tributary of James River, Midway Mills, Virginia, USA: E.R. Dunn; 15 November 1915. – KU 3254, 23 alch.; Pine Creek on Route 221, 2.8 mi. N.E. Floyd, Floyd County, Virginia, USA; R. Huffman, M.H. Ross & R.D. Ross; 4 May 1952. – KU 3259. 39 alch. and 8 C&S: Elliot Creek, tributary S. Rogers, Montgomery County, Virginia, USA; W. Davis, M.H. Ross & R.D. Ross; 13 April 1952. – KU 3265, 38 alch.; N. Fork Roanoke River at Route 11 bridge, Montgomery County – Roanoke County line. Virginia, USA; B. Stouth, T. Riggin & W.S. Davis; 17 May 1952. – KU 3275, 14 alch.; Catawa Creek, 6.6 mi. N. W. Salem on Route 311 (James River system), Roanoke county, Virginia, USA; E.C. Raney & R.D. Ross; 14 July 1954. – KU 22257, 22 alch.: Craig Creek at Va. Rout 621. Montgomery County, Virginia, USA; B.K. Wagner et al; 9 September 1987. – KU 22295, 35 alch.; Blackwater River at Rt. 641 bridge, Franklin County, Virginia, USA; B.K. Wagner et al.; 13 September 1987. – UT 44.239. 5 alch.; Elliot Creek at Rogers. Montgomery County, Virginia, USA: Ross; 20 May 1953. – UT 44.3524, 13 alch.; Crab Creek at 18, Allegany County, North Carolina, USA; 21 May 1986; collector unknown; 1986. – UT 44.526, 45 alch.; Roanoke drainage. Falling River below bridge on Motrosa Farm, Campbell County, Virginia, USA; J. Striegel & S. Robertson; 1970.

Diagnosis (amended from Cope 1868)

A *Phoxinus* with side bearing one longitudinal stripe and 10 to 15 transverse bars. The lateral stripe interrupted or faded at middle of body, the transverse bars present dorsal to the lateral stripe. Ventral side of body from base of pectoral fin to anterior end of isthmus dark; lower jaw shorter than upper one, the former enclosed by the latter; very long intestine with about 10 loops, its length 278% of standard length; epibranchial 3 bearing a large notch and a long posterior process at its dorsoposterior margin; epibranchial 4 bearing a large notch at its posterior margin.

Description (Tab.8)

A North American species of *Phoxinus* with average standard length (adults) about 50 mm, maximum standard length 61 mm. Head moderately large, its length 25% and its width 58% of standard length. Snout length 34% of head length, and 100% of orbit length. Eye large; orbit length 28% of head length. Mouth subterminal, small and almost horizontal; its gape extending below anterior margin of eye. Lower jaw shorter than upper one.

Bony interorbital space wide, its width 119% of orbit length and 32% of head length. Anterior nasal opening elliptical and smaller than the semi-round posterior one.

Young individual (18.1 mm standard length) with axis of olfactory organ short and wide, not extending to middle portion of the organ, seven primary lamellae present; in adult (53.4 mm standard length), axis slender, elongate and extending posteriorly, 13 primary lamellae present. Gill rakers 8, short.

Tab.8: Body proportions (%) of *Phoxinus oreas*. (ACGL: anterior chamber of gas bladder length; BD: body depth; BIW: bony interorbital width; CPD: caudal peduncle depth; CPL: caudal peduncle length; HD: head depth; HL: head length; HW: head width; IL: intestine length; Number: number of specimens; OL: orbit length; PCGL: posterior chamber of gas bladder length; PRDL: predorsal fin length; PRPL: prepelvic fin length; S: standard deviation; SL: standard length; SNL: snout length).

	HL/SL	HD/SL	BD/SL	CPL/SL	CPD/SL	PRDL/SL	PRPL/SL	IL/SL	HW/SL	HD/HL
Number	15	15	15	15	15	15	13	2	15	15
	23.3	14.9	19.3	18.9	9.5	53.3	46.8	276.9	12.7	57.5
Range	–	–	–	–	–	–	–	–	–	–
	27.9	18.2	24.8	25.2	13.1	60.1	50.9	279.4	17.8	68.5
Mean	25.4	16.5	22.3	23.3	11.1	56.7	48.8	278.2	14.6	64.9
S(±)	1.2	1.0	3.2	1.8	1.1	2.3	2.1	1.8	1.3	4.1

	OL/HL	HW/HL	SNL/HL	BIW/HL	BIW/OL	SNL/OL	PRDL/ PRPL	CPD/CPL	ACGL/ PCGL
Number	14	15	15	15	15	15	13	15	4
	25.8	50.4	30.2	27.5	91.1	80.6	109.0	39.1	38.8
Range	–	–	–	–	–	–	–	–	–
	31.2	69.9	39.0	32.3	148.6	121.6	128.5	52.9	85.7
Mean	28.4	57.7	34.2	30.2	118.8	99.7	117.0	47.9	65.5
S(±)	2.6	4.7	2.6	2.7	16.1	12.9	5.2	5.2	5.0

Maximum depth of body 23% of standard length. Caudal peduncle short and high, its length 23%, its depth 48% of standard length.

Genital papilla small. In male, papilla slender with a posterior projection; margin of genital orifice serrated; ventral surface smooth without skin fold. In female, genital papilla short and broad without posterior projection; margin of genital orifice serrated.

Pectoral fin fan-like; sharper in female; with 13-16 rays, usually 14 or 15. Pelvic fin originates in advance of dorsal fin origin; prepelvic length 49% of standard length; pelvic rays usually eight, seven in two of the 16 specimens counted.

Dorsal fin originates posterior to pelvic fin origin, predorsal length 57% of standard length, 117% of prepelvic length; with two procurrent rays and eight rays, occasionally seven (two of the 16 specimens counted with seven rays). Anal fin originates under or slightly behind insertion of dorsal fin, with one or two procurrent rays and 7-8 rays, mostly eight, only one among 16 specimens with seven rays. Caudal fin shallowly forked, lobes round or somewhat acute; with 9-11 dorsal procurrent rays, 7-10 ventral procurrent rays, and 19 (10+9) principal rays.

Small individuals (≤ 20 mm standard length) lack cephalic lateral line pores. Left and right supratemporal canals short without connection between each other, with six pores. Otic canal with six pores. Supraorbital canal with an interruption, 10 pores. Infraorbital canal without interruption, 14 pores. Preopercular canal extending to middle of preopercle, seven pores. Mandibular canal with five pores.

Body lateral line extending from dorsal to gill cover, gradually curving down to horizontal lateral stripe, and ending above the middle region of pectoral fin. Lateral line with one or two interruptions, 15 pored scales present.

Pharyngeal bone slender; pitted surface bearing about seven fossae; anterior limb long and slender, its anterior end flat and expanding; posterior limb straight. Pharyngeal teeth in one row, 5-5; teeth relatively short, hooked at tip.

Vertebrae 38-39; precaudal ones 20 or 21, caudal ones 18.

Intestine long, about 10 loops in adults, the most complex coiling pattern in *Phoxinus*. Its length 278% of standard length. This coiling type formed very early ontogenetically, as observed in specimens at about 18 mm standard length. Anterior chamber of gas bladder short, about 66% of posterior one in length. Pneumatic duct placed at the constriction. Peritoneum dark.

Tuberculation. Entire body, including lateral, dorsal, and ventral sides of body and head, bearing tubercles. Each scale of the six to eight rows of the breast scales (four rows observed in one specimen) bearing 3 or 4 tubercles in one row at apical margin of scale. Each anteroventral scale bearing fewer tubercles than each lateral scale; ventral side of the body between base of pectoral fin and the origin of anal fin lacking tubercles. Each scale at anterolateral body bearing one large tubercle; each scale on the posterior portion of body, especially on ventral side of caudal peduncle, bearing three or four tubercles in one row on its apical margin. Dorsal side of the second to fifth ray of pectoral fin bearing two rows of tubercles; other pectoral rays bearing smaller and fewer tubercles, no tubercles on interradial membranes. Ventral side of pectoral fin bearing fewer and smaller tubercles than on the dorsal side. Ventral side of the pelvic fin bearing tubercles; fewer tubercles on the dorsal side than on the ventral one of the pelvic fin. Anal and dorsal fins bearing few tubercles. No tubercles present on caudal fin.

Coloration. One lateral dark stripe, and 10-15 transverse bars present on trunk. Lateral stripe ventral to transverse bars (without contacting the stripe). Lateral stripe uniform in width throughout its length. Stripe extends through eye, opercle, and along body, to end at base of caudal fin. No dark spots present at caudal fin base. Transverse bars short, almost evenly present at trunk from posterior to the opercle membrane's posterior margin to the caudal fin base. In some specimens, about 10 dark short bars cross body dorsum, but not connecting the lateral bars. A dorsal stripe from nape to dorsal side of caudal fin not present in these specimens. In other specimens, however, one dark dorsal stripe extending from nape to base of caudal fin, the "crossing stripe" mentioned above not present in these specimens. Numerous melanophores present dorsally to horizontal lateral stripe. No melanophores present ventrally to horizontal stripe, except anteroventral portion of body. Numerous melanophores at anteroventral part of body, from anterior portion of lower jaw to pectoral fin base. Anterior end of the lower jaw bearing more melanophores than rest of ventral side of head. All fins bearing melanophores. First four to five pectoral fin rays bearing more melanophores than other pectoral fin rays. In caudal, anal, and pelvic fins, melanophores almost evenly present on the fins.

Biology

P. oreas occurs in small to medium size rivers. It is present in cool to warm, rapidly to slowly flowing, clear to turbid environments with sandy to rocky bottom (Starnes & Starnes 1980C; Page & Burr 1991). Fish species associated with this dace include *Notropis cerasinus, N. ardens* (Raney 1947), *Semotilus atromaculatus, Clinostomus funduloides, Nocomis leptocephalus*, and *Rhinichthys atratulus* (Maurakis & Woolcott 1992). Hybrids of *P. oreas* x *Semotilus* have been reported (Hamtrick 1977, Maurakis & Woolcott 1992).

The diet of *P. oreas* is unknown, but it was thought to be similar to that of *P. erythrogaster* and *cumberlandensis* by Starnes & Starnes (1980c).

The spawning season of *P. oreas* is in spring and early summer, using the nest of *Nocomis*. Up to 30 males might share one single nest. In most cases, more than one male follows one female during spawning (Raney 1947).

Distribution

P. oreas occurs in a belt-like area in the mountains of eastern North America. It was found from Virginia in the north, to North Corolina in the south. This species is also present in upper Tennessee drainage of Virginia and Tennessee (Stauffer et al. 1975, Starnes & Starnes 1980, Jowswiak et al. 1980).

Etymology

The epithet *oreas* is a Latin word meaning "of the mountains". It probably was chosen to indicate the primary habitat of the species.

Phoxinus eos (Cope, 1862)

Synonymy

Chrosomus eos Cope, 1862 – Cope 1862: 523 (orig desc., type locality: Meshoppen Creek, Susquehanna County, Pennsylvania); Cope 1868: 233 (comparison with *P. oreas*); Cope 1869: 375, 391 (desc., dist., Pennsylvania); Jordan 1877: 71 (name); Jordan & Gilbert 1882: 154 (Susquehanna River, Pennsylvania); Jordan & Swain 1883: 248 (name); Jordan et al. 1930: 113 (east of the Alleghenies, north to the Susquehanna River, Pennsylvania); Toner 1933: 137 (name); Lindeborg 1941: 160 (Ontario, Canada); Hubbs & Lagler 1949: 57, 64, fig.131 (whole body) (Great Lakes region); Scott 1957: 161 (Canada); Underhill 1957: 13, 25, 28, map 7 (dist., Minnesota); Bailey & Allum 1962: 41-42, 120, tab. 9 (dist., South Dakota); New 1962: 147, 149, 151, tab.1, figs. 1-6 (external morphology); Phillips 1969a: 501, 506-509, tab.2B, 3-4, fig.2 (external morphology and variation, Minnesota); Legendre 1970b: 1167, 1172, 1174-1176, tab.I, figs.1-2, 4-6 (Mendelian, Canada); Eddy & Underhill 1974: 239, fig.74 (key); Mahy 1975c: 618-634, tab.1, figs.1-3, 6, 8-12, 14-22 (osteology); Settles & Hoyt 1978: 297 (name); Gaswoska 1979: 373, 381, 383, 392-393, figs.5, 19, 31, 38, 43, 49, 61, 81 (osteology); Böhlke 1984: 75 (type specimens in ANSP).

Chrosomus eos (Cope) – Woronecki 1969: 709-710 (dist., Prince Edward Island, Canada).

Phoxinus eos (Cope) – Legendre & Steven 1969: 913, tabs. 1-2 (chromosome 2N=50); Legendre 1970a: 325, 329, tabs.1-2 (numbers of vertebrae); Mahy 1972: 728 (taxonomic status); Mahy 1975c: 617, 635-639 (taxonomic status); Starnes & Starnes 1978: 509, 513 (name); Joswiak 1980: 2, 3, 5-7, 15, 17-22, tabs.2-5, fig.2 (chromosomes); Joswiak et al. 1980: 913 (name); Stasiak 1980a: 336, figs. p.336 (no figure number) (general review); Starnes & Starnes 1981: 362 (name); Joswiak & Moore 1982: 399-400, fig.1 (discriminant analysis); Joswiak et al. 1982: 968, 972, tab.1 (external morphology); Cooper 1983: 112, 113, fig. p.113 (dist., Pennsylvania); Constantinescu et al. 1984: 286, tab.1 (coloration and behavior comparison with other *Phoxinus* species); Howes 1985: 71 (name); Coad 1987: 45 (dist., Ottawa, Canada); Dawley & Goddard 1988: 649-657, tab.1 (chromosomes); Harbicht et al. 1988: 475, tab.2, fig.2 (new records, Manitoba, Canada); Naud & Magnan 1988: 1249, figs.1, 2 (food and migration); Starnes & Jenkins 1988: 517 (name); Das & Nelson 1989: 579, 581-583, figs.1A, 2 (Alberta, Canada); Goddard et al. 1989: 268, 271-277, fig.1, Appendix (chromosomes); Goddard & Dawley 1990: 1052-1063, tab. 1 (New Hampshire); Dawley et al. 1991: 275-182 (chromosomes); Mayden 1991: 260 (name); Nelson & Paetz 1992: 151, 153, 154, fig. p.151, map. 12.8 (dist., Alberta, Canada).

Phoxinus erythrogaster eos (Cope) – Jordan & Evermann 1896: 244 (name); Fowler 1908: 520 (Pennsylvania); Mahy 1972: 729 (taxonomic status); Mahy 1975c: 618, 839, fig.22 (taxonomic status).

Material studied

Paratypes: ANSP 22117, 2 alch.; Meshoppen Creek, Susquehanna County, Pennsylvania, USA; E.D. Cope; September 1861.

Other Specimens: AMNH 21741sw, 2 C&S; Poeace River, Charlie Lake, British Columbia, Canada; Lindsey & Larkin; 12 August 1954. – AMNH 42403, 6 alch.; Mettawee Creek just west of Raceville, Washington County, New York, USA; C.L. Smith et al.; 1 June 1979. – ANSP 70840, 25 alch.; Beaver Pond, Mount Desert, Main, USA; H.W. Fowler; 3 July 1940. – ANSP 71725, 1 alch.; Buffalo Lake, Buffalo, Minnesota, USA; J. Boehlke; 29 September 1945. – CAS (SU) 36992, 23 alch.; near Morse's Line, about on Canada border, Franklin County, Vermont, USA; L. Babbitt & A. Daugherty; 14 September 1941. – KU 1169, 4 alch.; Pond in Wilderness Park, Emmet County, Michigan, USA; U.B.S. Ichthyology Class; 24 July 1946. – KU 2130, 1 alch.; French River, St. Louis County, Minnesota, USA; collector unknown; 26 Aug 1946. – KU 8524, 13 alch.; Snake River, Cherry County, Nebraska, USA; R. Reckham; 21 August 1963. – KU 10316, 16 alch. and 2 C&S; Mississippi River at Itaska State Park, Clearwater County, Minnesota, USA; G.L. Phillips & C.E. Judd; 20 June 1965. – KU 11335, 31 alch. and 2 C&S; Seney National Wildlife Refuge, Schoolcraft County, Michigan, USA; W.L. Pflieger, 31 August 1958. – KU 12255, 30 alch. and 10 C&S; Small stream immediately below outlet of Spring Lake, west side of County road E., Sawyer County, Wisconsin, USA; F.B. Cross & W. Ayers; 25 July 1967. – UT 44.2889, 33 alch.; Crow Wing River, gravel road at outlet of 5th Crow Wing, Hubbard County, Minnesota, USA; D.A. & M.A. Etnier, W.C. & L.B. Starnes; 20 June 1982.

Diagnosis (amended from Cope 1862)

A *Phoxinus* with small mouth, its gape not reaching below anterior margin of eye; two lateral dark stripes present, the lower one more developed than the upper; no dark spots on dorsal part of trunk; axis of olfactory organ long and narrow; nasal bone expanded, triangular in shape; nasal portion of supraorbital canal running along lateral portion of nasal bone; hyoid foramen formed by ventral hypohyal alone; urohyal base bearing a process at the posterior margin; basibranchial 4 present as a cartilage; interopercle with round posterior margin.

Description (Tab.9)

A North American species of *Phoxinus* with average standard length about 50 mm (adults), maximum 61 mm (Stasiak 1980a). Head moderately large, its length 27%, its width 55%, and its depth 22% of standard length. Snout short; its length 24% of head length, 83% of orbit length. Eye large, lateral on head; orbit length 30% of head length. Mouth terminal, small and oblique. Lower jaw slightly shorter than upper one.

Bony interorbital space wide, its width 118% of orbit length, 35% of head length.

Young individual (26.4 mm standard length) with short and broad axis of olfactory organ, the axis not reaching to middle of organ, seven primary lamellae present; adult individu-

Tab.9: Body proportions (%) of *Phoxinus eos.* (ACGL: anterior chamber of gas bladder length; BD: body depth; BIW: bony interorbital width; CPD: caudal peduncle depth; CPL: caudal peduncle length; HD: head depth; HL: head length; HW: head width; IL: intestine length; Number: number of specimens; OL: orbit length; PCGL: posterior chamber of gas bladder length; PRDL: predorsal fin length; PRPL: prepelvic fin length; S: standard deviation; SL: standard length; SNL: snout length).

	HL/SL	HD/SL	BD/SL	CPL/SL	CPD/SL	PRDL/SL	PRPL/SL	IL/SL	HW/SL	HD/HL
Number	16	15	15	15	16	16	16	4	16	16
Range	25.1 – 29.3	15.5 – 19.6	18.2 – 26.1	22.7 – 27.9	8.2 – 12.5	55.3 – 61.1	47.4 – 53.0	131.0 – 14 0.2	11.4 – 17.5	55.9 – 67.6
Mean	26.7	21.5	16.4	25.2	10.6	55.6	51 .4	134.8	14.5	61.8
S(±)	1.4	1.1	2.4	1.8	1.1	5.7	2.5	4.4	1.5	5.4

	OL/HL	HW/HL	SNL/HL	BIW/HL	BIW/OL	SNL/OL	PRDL/ PRPL	CPD/CPL	ACGL/ PCGL
Number	16	16	16	16	16	15	15	15	4
Range	28.3 – 35.6	43.4 – 62.4	20.5 – 27.6	30.8 – 41.0	108.0 – 146.7	72.0 – 100.0	98.3 – 119.1	3 6.5 – 51.4	62.5 – 68.3
Mean	29.8	54.7	23.8	34.8	118.3	82.5	1 11.2	43.2	65.1
S(±)	3.5	6.9	1.9	3.2	14.9	9.9	6.1	5.1	2.55

al (45.0 mm standard length) with a slender, elongated axis extending posteriorly, and 10 primary lamellae.

Body elongate, round in cross section. Maximum depth of body 16% of standard length. Caudal peduncle short and high, its length 25%, its depth 43% of standard length.

Pectoral fin fan-like, sharper in female than in male, 13-16 fin rays, 14 or 15 rays in most specimens studied. Pelvic fin originates in advance of dorsal fin origin; prepelvic length 51% of standard length; rays usually eight, seven in two among 16 specimens counted.

Dorsal fin originates posteriorly to origin of pelvic fin, predorsal length 111% of prepelvic length, with two procurrent rays and eight rays, rarely seven (two of the 16 specimens counted). Anal fin originates under or slightly behind the insertion of dorsal fin; with two procurrent rays eight, rarely seven (one among 16 specimens counted). Caudal fin shallowly forked, lobes round; with 8-12 dorsal procurrent rays, 7-9 ventral procurrent rays, 19 (10+9) principal rays.

Supratemporal canal short, without connection between the left and right ones, with six pores. Otic canal, with six pores, connecting with infraorbital canal and body lateral line; however, in a few specimens, no connection between otic canal and body lateral line present. Supraorbital canal with 10 pores. Infraorbital canal without interruption, 14 pores. Preopercular canal extending to middle portion of preopercle; with seven pores. Mandibular canal with interruption, not connecting with preopercular canal, five pores.

Body lateral line extending from dorsal to gill cover, curving down to ventral lateral stripe, and ending at position of middle of pectoral fin. Lateral line interrupted in a few places, most with one or two interruptions. Lateral line pored scales about 17.

Pharyngeal bone short, posterior limb bent; pitted surface bearing two large, elongate fossae; end of anterior limb bearing a notch. Pharyngeal teeth in one row, 5-5, 5-3, or 5-4; teeth elongate, hooked at tip. Gill rakers 8, short.

Vertebrae 37-39; precaudal vertebrae 20-21, caudal vertebrae 17-18.

Intestine long, with complex coils; its length 135% of standard length. Anterior chamber of the gas bladder short, 65% of posterior chamber in length. Pneumatic duct placed at the constriction of the gas bladder. Peritoneum dark.

Tuberculation. Tubercles present on whole body, including lateral, dorsal, and ventral sides, dorsal and lateral sides of head, snout and chin. Each scale in 5-7 rows on breast bearing a few tubercles at its apical margin. Scales on the ventral side other than the breast scales bearing fewer tubercles than scales on sides. Each scale on the anterolateral body bearing one or two rows of tubercles: one row near apical margin, and composed of two or three tubercles; and another row close to center of scale, consisting of one to three tubercles. Tuberculation of pectoral, pelvic, dorsal and anal fins similar to that in *Phoxinus cumberlandensis*. No tubercles on caudal fin.

Coloration. Two dark lateral stripes present on sides. Lower lateral stripe more developed than upper one, and extending from anterior end of snout, through eye, gill cover, and along side to terminate in a black spot at caudal fin base. Stripe almost equal in width throughout its length. Upper lateral stripe shorter than lower one, and interrupted into a series of spots behind dorsal fin origin; or the whole stripe broken down to large speckles. Upper lateral stripe beginning dorsally to dorsoposterior margin of opercle, extending almost parallel to lower stripe, and terminating on posterior part of caudal peduncle. A dark mid-dorsal stripe begins at nape and ends at dorsal side of caudal fin base. Dorsal stripe behind insertion of dorsal fin narrower than anterior to dorsal fin origin. Dorsal stripe not evident in specimens less than 25 mm standard length, but lateral stripes occur in these small individuals.

No melanophores present at chin, except on anteroventral side of lower jaw, which bears dense melanophores. Numerous melanophores present dorsal to upper lateral stripe, and on area between upper and lower lateral stripes. No melanophores present ventral to lower lateral stripe, except in a small area near pectoral fin base, and on ventral edge of caudal peduncle.

Numerous melanophores present on fins. First four or five pectoral rays bearing more melanophores than other rays, especially in breeding males. Melanophores almost evenly present on pelvic, anal, and caudal fins. On dorsal fin, base bearing more melanophores than other portions of fin. A black spot present at caudal fin base.

Biology

Biology of *Phoxinus eos* has been studied by numerous ichthyologists from the 1930's to the 1980's though it is still not well known. Cooper (1935) and Hubbs & Cooper (1936) studied the reproductive behavior; Tyler (1966) studied lethal temperature; Scott & Crossman (1973), Stasiak (1978), and Cooper (1983) studied the general biology of the species. The following description is a summary of those publications.

P. eos occurs in bog ponds, lakes and creeks, but prefers quiet water (Cooper 1983). The fish species found associated with *P. eos* include *P. neogaeus, Pimephales promelas, Umbra limi*, and *Culaea inconstans* (Stasiak 1978). Hybrids of *P. eos x P. neogaeus* are common in localities; however, for some reasons, only one parent species was found in these localities (Hubbs & Brown 1929, New 1962, Legendre 1970b, Stasiak 1979, Joswiak, Stasiak & Moore 1982, Das & Nelson 1989, Goddard & Dawley 1990).

Food of *P. eos* is composed of algae, zooplankton and aquatic insects (Scott & Crossman 1973; Cooper 1983). Cooper (1935) reported that the adult dace was observed eating smallmouth bass fry.

Maturity of the species is reached in the second summer of life (Cooper 1983). Spawning begins in spring or early summer. Cooper (1935) and Hubbs & Cooper (1935) described that spawning activity occurs from late May to August in Michigan. Females with large eggs were caught in August by McPhail & Lindsey (1970). Hubbs & Cooper (1935) suggested some females might spawn at least twice in a single summer season. Cooper (1935) described a complicated reproductive behavior of *P. eos*.

Distribution

Stasiak (1980a) compiled the distribution data, indicating the range from Nova Scotia and Prince Edward Island (Canada), the St. Lawrence basin, and Atlantic drainage of New England, west to Peace-Mackenzie drainage in British Columbia and Northwest Territories, South to upper Missouri River drainage in the Great Plains.

Etymology

The epithet *"eos"* is a Latin word, meaning "down", or "sunrise". It might refer to the color pattern of the breeding males (Nelson & Paetz 1992).

Phoxinus erythrogaster (Rafinesque, 1820a)

Synonymy

Chrosomus eos (Cope) – Underhill 1957: map 7 (mis.id., Messota; based on Phillips 1968).

Chrosomus erythrogaster (Rafinesque, 1820) – Rafinesque 1820a: 237 (name); Fowler 1904: 244 (dist. Rogers, Arkansas); Fowler 1908: 519 (Pennsylvania); Toner 1933: 137 (name); Koster 1939: 203, 205-206 (behavior); Jennings 1942: 365 (Kansas); Hass 1943: 162 (Illinois); Harlan & Speaker 1951: 75, 192, 216, pl.14 (whole body) (Mississippi River drainage in Iowa); Hubbs & Bailey 1951: 145, 148-151, tabs.I, II (Illinois); Underhill 1957: 13, 25, 29, map 7 (Minnesota); Minckley 1959: 419, 436, tab. 3 (Kansas); Cross & Minckley 1960: 3-4, 6-7, tabs.1-2 (Kansas); Cross 1967: 70, 81-83 (Kansas); Phillips & Etnier 1969: 96, 97, tab.1 (Minnesota); Phillips 1969b: 99, 101, 104, 106-108, tabs.1-3 (diet, Minnesota); Phillips 1969c: 524-525, tab.1 (Fecundity, Dodge County, Minnesota); Stasiak 1972: 3, 34, 43 (name); Mahy 1975c: 617-634, tab.1, figs.1-3, 6, 8-21 (osteology); Freeze & Rayburn 1977: 97 (dist.: Kentucky).

Chrosomus erythrogaster Rafinesque, 1820 – Rafinesque 1820b: 48 (name); Cope 1862: 523 (comparison with *Phoxinus eos*); Cope 1864: 281 (comparison with *P. neogaeus*); Cope 1869: 375, 390-391, fig. (pharyngeal bone and teeth), (desc., dist., Pennsylvania); Jordan & Swain 1883: 248 (Whitley County, Kentucky); Jordan & Evermann 1896: 244 (dist.: New Brunswick to Ohio, Michigan, Iowa, and Northern Alabama); Rafinesque 1899: 102 (name); Smith 1908: 9, figs.1-3 (spawning behavior, Illinois); Cockerell & Callaway 1909: 122 (scales); Forbes & Richardson 1920: 112, 113, 114, fig. (dist., Illinois); Hankinson 1923: 30 (New York); Fowler 1924: 391 (desc., dist., Holston River, Virginia; Illinois; Miami River, Indiana; Delhi, Iowa; Marshfield, Missouri and Rogers, Arkansas); Hubbs & Brown 1929: 28, 29 (dist., Ontario, Canada); Jordan et al. 1930: 113 (dist.: New Branswick to Ohio, Wisconsin, Colorado and Northern Alabama); Welter 1938: 68 (Kentucky); Hubbs & Lagler 1949: 57, 64, fig. p.132 (whole body) (dist., Great Lakes region); Hill & Jensen 1968: 55, tabs.1, 2, fig.1 (external morphology, Oklahoma); Phillips 1969a: 501, 506-507, tabs.2A, 4, fig.2 (morphology and variation, Minnesota); Wiley & Collette 1970: 168 (name); Hubbs & Echelle 1972: 150 (Arkansas System, New Mexico); Greenfield et al. 1973: 54-59, tabs.1-3, figs.1-5, 7 (morphology); Eddy & Underhill 1974: 238, 239, figs.73 (whole body), 74 (head); Settle & Hoyt 1978: 290, 295, tab.1, figs.1, 2 (reproductive biology, Kentucky); Gasowska 1979: 373-374, 381, 383, 392, 399-400, 402, fig.4, 18, 30, 54, 76, 80, pl.1 fig.5 (osteology).

Chrosomus erythrogaster erythrogaster Rafinesque – 1951 Bailey 1951: 193, 216 (Iowa).

Chrosomus pyrrhogaster Jordan – Jordan 1877a: 71 (North Indiana); Mahy : 618 (name).

Leuciscus erythrogaster (Rafinesque) – Günther 1868: 247 (desc., dist., Ohio, Michigan).

Luxilus erythrogaster Rafinesque, 1820 – Rafinesque 1820a: 237 (orig. desc.; type locality: Kentucky River, Kentucky). [The Kentucky River might be a small tributary (Starnes & Starnes 1980b).]

Phoxinus erythrogaster (Rafinesque) – Phillips 1968b: 565 (new records, Missouri River, Minnesota); Pflieger 1971: 331, map 33 (dist., Ozark and Lincoln county, Missouri); Mahy 1972: 728 (name); Cross & Collins 1975: 47, fig. p.47, map p.47 (dist., Kansas); Pflieger 1975: 97, 132, map p.132 (dist. Missouri); Mahy 1975c: 635-639, fig.23A (taxonomic status); Frazier & Beadles 1977: 39 (dist., Stone County, Arkansas); Starnes & Starnes 1977: 2 (dist., Upper Cumberland River); Starnes & Starnes 1978: 508, 512-513, 515, figs.2B, 3C (comparison with *P. cumberlandensis*); Smith 1979: 130, 131, figs. p.130 (whole body), and 131 (dist. map) (northern Illinois); Joswiak 1980: ii, 2-3, 5-6, 13, 15-20, 22, tabs.2, 4-5, fig.2 (chromosome); Joswiak et al. 1980: 914 (name); Starnes & Starnes 1980b: 337, fig. and map p.337 (general review); Starnes & Starnes 1981: 362, 365-368 (name); Trautman 1981: 306-308, fig.53 (whole body), map 53 (dist., Ohio); Joswiak & Moore 1982: 398-400, fig.1 (discriminant analysis using Phillips' 1969 data); Cooper 1983: 112-114, fig. and map p.113 (Pennsylvania); Constantinescu et al. 1984: tab.1 (coloration, behavior, and comparison with other *Phoxinus* species); Robinson & Buchanan 1984: 245, 246, figs. p.245, 246 (White, Black, and Illinois Rivers, northern Arkansas); Howes 1985: 57-72, figs.1B and D, 2C, 7D (systematics); Starnes & Etnier 1986: tab.10.1 (Tennessee River, Cumberland River); Cross & Moss 1987: tab. 20.1, 20.3 (Kansas); Starnes & Jenkins 1988: 517, 524, 525, 528 (name); Mayden 1989: 17, 33, 141 (name); Mayden 1991: 260 (name); Hearald (year unknown): 90 (name).

Phoxinus erythrogaster erythrogaster (Rafinesque) – Mahy 1972: 728 (osteology); Mahy 1975c: 618, 640, fig.22 (taxonomic status).

Material studied

AMNH 21743sw, 3 C&S; White Eyes Creek, Monroe Township, Muskingum County, Ohio, USA; C.L. Smith et al.; 11 August 1963. – AMNH 42937sw, 2C&S; Deep Creek at Rt. I-70, Wabaunsee County, Kansas, USA; R. Irwin; 7 June 1966. – AMNH 52488, 10 alch.: White Eyes Creek, Monroe Township, Muskingum County, Ohio, USA; C.L. Smith et al.; 11 August 1963. – ANSP 4182, 1 alch.; Kiskiminitas River, western Pennsylvania, Pennsylvania; E.D. Cope; date unknown. – ANSP 5479, 4 alch.; Miami River, Indiana, USA; E.D. Cope; date unknown. – ANSP 54567, 6 alch.; Near Bear Creek, Allandale, Ontario, Canada; G. & E. Johns and J.G. Carison; 31 July 1927. – ANSP 83178, 40 alch.; Indian Creek at Walnut Hill, Lee County, Virginia, USA; F.G. Thompson; 27 September 1953. – ANSP 84333, 2 alch.; Franmlin Twp., Tributary North Branch of Salt Creek, 3.5 mi. East of Moreland, Wayne County, Ohio, USA; F.G. Thompson & Maly; 5 January 1953. – ANSP 84345, 13 alch.; Wayne Twp., 1.25 mi. Northeast of Wayne, Ashtabula County, Ohio, USA; F.G. Thompson; 18 October 1953. – ANSP 147537, Red River at mouth of first tributary below Rt. 77 bridge, Powell-Menifee County; Kentucky, USA; R.J. Horwitz; 18 April 1981. – CAS (SU) 05359, 28 alch.; Albany Branch, Clinton County, Kentucky, USA; U.S. fish Commission; date unknown. – KU 5773, 4 C&S; Pigeon Creek, Dent County, Missouri, USA; D.A. Distler; 19 June 1960. – KU 7300, 20 alch.; Pecatonica River, Sec. 13, T5N, R1E, Iowa County, Wisconsin, USA; F.B. Cross & R.

Poff; 14 June 1962. – KU 7606, 1 C&S; Pigeon Creek, Sec. 7-8, T32N R7W, Dent County, Missouri, USA; F.B. Cross et al.; 7 April 1963. – KU 10629, 12 alch. and 2 C&S; Possum Trot Creek, 3.25 mi. NE Dillard, T35N, R2W, S16. Crawford County, Missouri, USA; W.L. Pflieger & S. Cliburn; 18 July 1963. – KU 12495, 3 C&S; North Fork White River, Sec. 7, T27N, R11W, Douglas County, Missouri, USA; G.R. Smith et al.; 24 May 1967. – KU 12496, 5 C&S; North Fork White River, Sec. 7, T27N, R11W, Douglas County, Missouri, USA; G.R. Smith et al; 24 May 1967. – KU 13198, 1 C&S; Deep Creek at Rt 70 crossing, Wabanusee County, Kansas; R. Irwin; 7 June 1966. – KU 22092, 12 alch.; Tryon Grove Road, Sec. 20, T46N, R8E, McHenry County, Illinois, USA; O.T. Gorman & M.G. Meyer; 26 July 1986. – KU uncat., about 70 alch. and 4 C&S; Barren Fork of Illinois River at Camp Egan (near Proctor), Adair County, Oklahoma, USA; W. Matthews & X. Chen; 27 April 1991.

Diagnosis (amended from Rafinesque 1820a)

A *Phoxinus* with two lateral stripes, the upper one interrupted on caudal peduncle; intestine elongate; pharyngeal teeth in one row; epural bone elongate.

Description (Tab.10)

A North American *Phoxinus* species with average standard length (adults) about 60 mm, maximum standard length up to 90 mm. Head large, broad, and robust, its length 25% and its width 52% of standard length. Eye lateral on head, moderately large, orbit length 26% of head length. Snout moderately elongated, its length 27% of head length, 102% of orbit length. Mouth small, slightly subterminal and oblique, its gape not extending to below anterior margin of eye. Lower jaw slightly shorter than upper one.

Bony interorbital space wide, its width 122% of orbit length, 32% of head length. Anterior nasal opening smaller and shorter than the elongated posterior one. Margin of anterior nasal opening erect, except its anterior portion; margin of posterior nasal opening not erect, except its anterior portion.

Young individuals (18.0 mm standard length or less) with axis of olfactory organ short and located at anterior margin of olfactory chamber, four primary lamellae present; larger individual (46.0 mm standard length or larger) with axis elongate and extending posteriorly, 12 primary lamellae present. Numerous melanophores present on primary lamellae in both young and adult specimens.

Body elongate, stout, not strongly compressed, caudal peduncle more compressed than anterior part of the body. Maximum depth of body 21% of standard length. Caudal peduncle length 24% of standard length, its depth 43% of its length.

In male, genital papilla small, surface smooth without skin fold. In female, genital papilla larger than that in male, its surface bearing a few skin folds. Posterior margin of papilla close to anal fin origin in both male and female.

Pectoral fin fan-like, sharper and smaller in female than in male. The distal tip of pectoral fin never reaching pelvic fin origin; with 13-17 rays, most with 15 or 16 rays. Pelvic fin originates in advance of dorsal fin origin, in anterior half of body, prepelvic fin length

Tab.10: Body proportions (%) of *Phoxinus erythrogaster*. (ACGL: anterior chamber of gas bladder length; BIW: bony interorbital width; CPD: caudal peduncle depth; CPL: caudal peduncle length; HD: body depth; HD: head depth; HL: head length; HW: head width; IL: intestine length; Number: number of specimens measured; OL: orbital length; PCGL: posterior chamber of gas bladder length PRDL: predorsal length; PRPL: prepelvic length; SL: standard length; S: standard deviation; SNL: snout length).

	HL/SL	HD/SL	BD/SL	CPL/SL	CPD/SL	PRDL/SL	PRPL/SL	IL/SL	HW/SL	HD/HL
Number	16	16	16	16	15	16	16	3	16	16
	21.1	14.0	16.8	19.7	8.2	51.7	44.0	170 .0	11.1	55.1
Range	–	–	–	–	–	–	–	–	–	–
	26.2	16.5	25.4	25.6	11.3	57.0	49.3	21 0.0	14.4	72.2
Mean	24.8	15.3	21.1	24.2	10.2	55.1	47 .3	193.3	12.6	62.4
S(±)	1.3	0.8	2.1	5.0	0.8	4.8	1.8	20.8	1.0	4.2

	OL/HL	HW/HL	SNL/HL	BIW/HL	BIW/OL	SNL/OL	PRDL/ PRPL	CPD/CPL	ACGL/ PCGL
Number	16	16	16	16	16	16	16	16	3
	20.3	47.1	25.5	26.8	100.0	87.9	107.6	36.4	67.0
Range	–	–	–	–	–	–	–	–	–
	30.6	61.1	32.5	34.3	132.3	135.5	117.5	47.2	73.0
Mean	26.4	51.6	26.7	31.8	122.2	102.3	113.2	43.3	70.0
S(±)	3.1	5.2	2.1	2.6	14.6	14.0	4.3	4.0	4.32

47% of standard length; pelvic rays usually eight, one of 16 specimens counted with seven rays.

Dorsal fin originates posterior of origin of pelvic fin, in posterior half of body, predorsal length 55% of standard length, 113% of prepelvic length; procurrent rays two, eight rays in all specimens. Anal fin originated slightly behind insertion of dorsal fin; procurrent rays two; eight rays. Caudal fin deeply forked, lobes round; with nine or 10 dorsal procurrent, nine or 10 ventral procurrent rays, and 19 (10+9) principal rays.

Left and right supratemporal canals not connected, but close to each other in adults; with 16 pores. Otic canal connecting with infraorbital canal and lateral line; six pores. Supraorbital canal with 11 pores. Infraorbital canal without interruption; 18 pores. Preopercular canal extending to middle portion of the preopercle, without branch; 10 pores. Mandibular canal without interruption and branch, and without connection with preopercular canal; with five pores.

In adults, body lateral line extending from dorsal of gill cover, gradually curving down to and following lower lateral stripe, ending near posterior margin of pelvic fin. Lateral line shorter in young than in adults. Lateral line uninterrupted in adults, but with one or two gaps in young individuals. Lateral line scales 43.

Pharyngeal bone well developed and robust, its pitted surface broad with three large fossae. Posterior limb short, strong, and bent anteriorly. Anterior limb slender, narrower posteriorly, and expanding at anterior end. Pharyngeal teeth in one row, 5-5. Teeth strong, hooked at tip.

Vertebrae 37; precaudal vertebrae 20, caudal vertebrae 17.

Intestine long, with about 3.5 loops. Its length 193% of standard length. Gas bladder broad and relatively short. Anterior chamber round at anterior end, and almost equal in width for whole chamber. Posterior chamber almost equal in width from anterior to posterior ends. Anterior chamber 70% of posterior chamber in length. Constriction short and broad. Pneumatic duct placed at middle of the constriction. Peritoneum dark.

Tuberculation. **Male** Whole head, including its dorsal, lateral, and ventral sides, bearing tubercles. Tubercles on head small and short. Dorsum of head bearing higher density of tubercles than rest of body. Each scale in 10 or 11 rows on the breast bearing two to four tubercles on its apical margin, forming comb-like edge. All tubercles in this region similar in size and shape. Dorsal, lateral, and ventral sides of the body bearing tubercles. Each scale bearing one or two small, short tubercles near center of the scale, except in ventrolateral portion of the caudal peduncle. Every scale on the ventrolateral part of the caudal peduncle bearing one row of four to six well-developed tubercles on apical margin.

All fins except caudal fin bearing tubercles. Pelvic, dorsal, and anal fins, and ventral side of the pectoral fin have few small, short tubercles on fin rays and membrane. On pectoral fin, dorsal side of the second to seventh fin rays bearing two rows of well developed, sharp tubercles on its distal portion, decreasing to one row proximally. Proximal one-third of pectoral fin without tubercles. Few small tubercles on interradial membrane of pectoral fin.

Female Females bearing very small tubercles, hardly descendible with naked eye. Anterior end of snout tuberculated. Entire lateral and ventral sides of body bearing tubercles. Each scale in these regions bearing one or two small tubercles near center of scale. Pectoral, pelvic, dorsal, and anal fins bearing few small tubercles on both membrane and rays.

Coloration. Two distinct lateral black stripes present on the flank. Lower one longer and broader than upper one. Lower lateral stripe extending uninterrupted from anterior end of snout to base of caudal fin; the stripe broader at middle portion of body. Upper lateral stripe originates dorsal to posterior margin of opercle, and extends to posterior portion of caudal peduncle, but not reaching caudal fin base. Upper lateral stripe almost equal in width along its length, but interrupted in its posterior portion, forming a series of dots. A few small speckles (smaller than pupil of eye) occur dorsal to the upper lateral stripe. In females, the lateral stripes narrower and fainter than that in males, especially upper lateral stripe. Body dorsum darker than flank, bearing a mid-dorsal dark stripe. Dorsal stripe originating at nape and extending to posterior end of body. In most specimens studied, the dorsal stripe is continuous posterior to dorsal fin, but is interrupted in three specimens. No melanophores on ventral side of the body, except the breast area in males bearing some melanophores. In female, lateral body, as a whole, paler than in male.

Head with numerous melanophores dorsally, diminishing laterally. Anterior end of snout bearing melanophores. Lower portion of lateral side of head without melanophores. Numerous melanophores along margin of lower jaw. Therefore, left and right lower lateral stripe on the body continuous as a black band crossing the anterior end of the snout and lower jaw. Numerous melanophores present on sides of body, except ventral to the lower lateral stripe. Area between upper and lower lateral stripes pale.

Melanophores present on all fins. On pectoral fin, rays bearing more melanophores than the membranes, the first ray darkest. The posterior three or four rays and membranes almost lacking melanophores. As a whole, distal part with more melanophores than proximal part. Pelvic fin-rays bearing more melanophores than membrane, and distal part bearing more melanophores than proximal part. Dorsal fin-rays and membrane bearing melanophores; all rays equally pigmented. Base of dorsal fin bearing more melanophores than rest of the fin, forming a black basal patch. All anal fin-rays and membrane, except the most posterior two rays and membrane, bearing melanophores. Caudal fin darkest of all fins. High density of melanophores on middle portion of caudal fin forms a slightly darker patch. A dark spot about size of pupil present at caudal fin base.

Biology

Phoxinus erythrogaster occurs in small, clear, and spring-fed streams (Cross 1967, Smith 1979, pers. obs.). This species prefers headwaters, and scarity of the permanent springs might limit the distribution of the species in the Plains region (Cross 1967, Smith 1979). This dace can be in schools of a dozen to a few hundred individuals (Smith 1908). The fish species associated with *P. erythrogaster* include *Semotilus atromaculatus, Notropis cornutus, Campostoma anomalum, Rhinichthys* sp. and *Cottus* sp. (Smith 1908, Cross 1967). A few hybrids of *P. erythrogaster* with other species have been described, including *P. erythrogaster x Luxilus cornutus* (Hubbs & Bailey 1951, Minckley 1959, Cross & Minckley 1960, Greenfield et al. 1973), *P. erythrogaster x Campostoma anomalum* (Hubbs & Bailey 1951), *P. erythrogaster x Notropis nubilus* (Phillips & Etnier 1969), *P. erythrogaster x Semotilus atromaculatus* (Cross & Minckley 1960), and *P. erythrogaster x Notropis pilsbryi* (Robinson & Miller 1972).

The diet of *P. erythrogaster* includes diatoms, algae, bits of macrophytes, and small aquatic insects (Forbes & Richardson 1920, Phillips 1969b, Cooper 1983). The dace obtains food by nibbling or sucking the surface slime from stone and other objects (Forbes & Richardson 1920).

The spawning season varies from April to June, depending on the locality: in northern population from late May to the mid-June, in southern population from April to June (Eddy & Underhill 1974, Settles & Hoyt 1978, Starnes & Starnes 1981). The fecundity was estimated from less than 700 (Settle & Hoyt 1978) to about 20,000 eggs (Philips 1969c). The dace can be mature during the first year (Settles & Hoyt 1978, Smith 1979). According to Smith (1908), this species has a complex breeding behavior.

Distribution

P. erythrogaster occurs widely from Minnesota and western Pennsylvania, southward to Arkansas and Alabama (Starnes & Starnes 1980). Isolated populations occur on Crowley

Ridge in the Mississippi Embayment, and along the eastern rim of Mississippi floodplain in Mississippi (Hemphill 1957), and near Reelfoot Lake, Tennessee (Starnes & Starnes 1980). These are considered the relic populations (Starnes & Starne 1980). In New Mexico and Colorado, isolated populations are present in the Arkansas River drainage (Koster 1957, Cross, pers. comm.). Starnes & Starnes (1980) summarized the distribution data and prepared a map showing the geographical distribution of the species.

Comments

No subspecies of this widely distributed species has been reported. Some local and regional intraspecific variation of the species was studied in Oklahoma by Hill & Jensen (1969), and elsewhere by Phillips (1968a, 1969a). The intraspecific variation seems not to be significant.

Smith (1979) considered *Oxygeneum pulverulentum* Forbes a synonym of *P. erythrogaster*. However, *O. pulverulentum* is a hybrid of *P. erythrogaster x Campostoma anomalum* (Hubbs & Bailey 1952).

Etymology

The epithet *erythrogaster* is a Greek word, meaning "red belly" (Pflieger 1975), referring to the ventral color of the breeding male.

ABSTRACT

Key Words: Cyprinidae, *Phoxinus*, Morphology, Osteology, Phylogeny, Taxonomy, Biogeography.

Phoxinus is a small sized genus of Cyprinidae and occurs in both North America and Eurasia. A detailed review on major literature related to *Phoxinus* showed that the definition, taxonomy, and composition of *Phoxinus* have changed since its first description by Rafinesque (1820a), due to the unclear phylogenetic relationships among *Phoxinus* and between *Phoxinus* and other minnow genera.

The phylogenetic relationships of *Phoxinus* and other related minnow genera at the base of the Chub clade were reevaluated based on 29 transformation series. The Hemitremian clade was recognized as a monophyletic group and supported by the anterior placement of the anterior anal pterygiophores. Eight genera are included in the Hemitremian clade, i.e., *Margariscus, Couesius, Semotilus, Hemitremia, Phoxinus, Eupallasella, Rhynchocypris*, and *Lagowskiella*, among which *Hemitremia* is the sistergroup of all other seven genera.

The non-osteological and osteological morphology and their variations were described and compared among *Phoxinus*, and between *Phoxinus* and the outgroups (i.e., *Eupallasella, Rhynchocypris*, and *Lagowskiella*). The monophyly of *Phoxinus* was supported by eight transformation series, such as the specific tuberculation on the breast scales in breeding

males, the presence of an anterior process of the basioccipital bone, and division of the preoperculomandibular canal. Nine species were recognized in *Phoxinus*, including *P. brachyurus, phoxinus, issykkulensis, neogaeus, tennesseensis, cumberlandensis, oreas, eos*, and *erythrogaster*.

Two-hundred and ten transformation series were analyzed and polarized based mainly on outgroup comparison to evaluate the phylogenetic relationships among species of *Phoxinus*. The phylogenetic relationships of the species within the genus *Phoxinus* were resolved based on the 210 transformation series by PAUP (v.3.0). In *Phoxinus*, two major groups were recognized as the *brachyurus*- and the *erythrogaster*-clade. The *brachyurus*-clade consists of the three Eurasian and one North American species: *P. brachyurus, issykkulensis, phoxinus*, and *neogaeus*. Members of the *erythrogaster*-clade are the other five North American species, i.e., *P. cumberlandensis, tennesseensis, oreas, eos*, and *erythrogaster*.

Three hypotheses on the geographic relationships of the freshwater fish faunae in North America and Eurasia were reviewed and compared. These are the "trans-Atlantic", the "old Pacific connection", and the "Bering land connection" dispersal hypotheses. None of these hypotheses could explain the geographic distribution of *Phoxinus*. A "Bering land connection" vicariant hypothesis was proposed here to interpret the genus' geographic distribution. The Bering land connection vicariant hypothesis proposed that the submergence of the Bering land bridge during the Miocene caused the speciation of the ancestor of *Phoxinus*, while the interruption of the bridge during the Pliocene split the ancestor of the *Phoxinus* species complex. This hypothesis was well supported by the alloelectrophoretic studies of Joswiak (1980). The speciation within the *erythrogaster*-clade and the *phoxinus* species pair might be due to some vicariant events and/or adaptation to the habitats.

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APPENDICES

Appendix I

Data matrix of 29 transformation series used to generate the hypotheses of phylogenetic relationship for hemitremians in Fig.18. Outgroup: Exoglossin Clade (Coburn & Cavender 1992). 0: plesiomorphic character; 1: apomorphic character.

Taxon	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Couesius	1	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0
Eupallasella	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0
Hemitremia	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1
Lagowskiella	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0
Margariscus	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0
Phoxinus	0	0	1	1	1	1	1	1	1	0	1	0	1	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0
Rhynchocypris	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
Semotilus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0

Appendix II

Character matrix used by PAUP to construct the cladogram for the genus *Phoxinus* in Figure 93. Outgroup: *Eupallasella*, *Rhynchocypris*, and *Lagowskiella*; 0: plesiomorphic character; 1, 2, 3: apomorphic characters. For TS numbers see Appendix III.

	111111111122222222223333333333444444444455555555556666666666777777777788888888889999999999
Taxon	123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789
Outgroup	000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
P. brachyurus	010000000101010101001010000010100010001010011111111000101000100000001010101010010100000101000100010
P. cumberlandensis	000101111200100110000100001000010100101010000100000111000100001011112001001100001000010000101001010
P. eos	001010110001000100000000011000000000010110011110000000000000001010110001000100000000011000000000101
P. erythrogaster	000011010010000000001000101000000100001111000110010010010000000000110100100000001000101000000100001 11
P. issykkulensis	000000110101010101001110000000011100000001200101011100001111100011010101010011100000000111000000120
P. neogaeus	000000001100001100111000000001110001011101010111101101110101000000000110000110011100000111000101110
P. oreas	000001110110000000001000000000000100111011100100000111000000000011101100000000010000000000001001110
P. phoxinus	101011001110101111112010010011200100100100000110101011010110100101102010101001110010101111000010110
P. tennesseensis	000000011000000000000010210001001111000011100000001110100011000000010010100000000010000010001001010

	111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111122222222222
	000000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999900000000001
Taxon	012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Outgroup	000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
P. brachyurus	100111111110001010000000001000001010000000001000000001000000000000000000000000100000010110000000000000001100101010
P. cumberlandensis	100001000000111000100011011101001011011011010000000000000000010001110001001001000000100001111010101001100000 01
P. eos	100111100000000000001000000110111110110101010001000000000011011110000010100001100010001001000011010011100000 00
P. erythrogaster	100011001001001001000000110000011011010101010110001001010000001011110100010010001111000001010000100011000000010
P. issykkulensis	010101110000011111010001011010001100000001001011000000101010100010000000000000100010010100000000000001111000 00
P. neogaeus	101011110110111010101000100000001110000110000000000110000001001000000000000001000011001000100000000011111000000
P. oreas	111001000000111000000000000000010111000011101111000100000000010000100000000000000101010000000000100000000000101
P. phoxinus	001000100110101010100000111110010000000011100111011110100100010001000100011010100010011010000100100000010000 00
P. tennesseensis	101011100000111000100001001000001011100000010010000000000000100001100000000010010001001000000000000001100110100

Appendix III

The transformation series used in the analysis of the phylogenetic relationship within the genus *Phoxinus*. The transformation series numbers corresponding to the TS numbers in the text (page 44-141) and Appendix II. [0] = plesiomorphic, [1], [2], [3] = apomorphic character.

1) Mouth angle small (≤55°) [0] (Fig.19A), or large (≤60°) [1] (Fig.19B).

2) Mouth gape not extending to [0] (Fig.19A), or extending to [1] (Fig.19B) below the middle of eye pupil.

3) Dorsal side of nasal septum on the bridge between the anterior and posterior nasal openings smooth [0] (Fig.20B), or concave [1] (Fig.20A).

4) Middle portion of the anterior margin of anterior nasal opening erect [0] (Fig.20A), or unerect [1] (Fig.20B).

5) The highest portion of the dorsal margin of primary lamellae of the olfactory organ distant from the axis [0] (Fig.21C), or close to the axis [1] (Fig.21A, B).

6) Fewer (about 10) [0], or more (about 16) [1] primary lamellae in the olfactory organ present (Tab.1).

7) Elongated ellipsoidal type [0] (Fig.21A, B), or linear type [1] (Fig.21C), or shorted ellipsoidal type [2] (Fig.21E) of axes of the olfactory organ.

8) Body lateral line extending to the caudal peduncle [0] (Fig.22F), or not [1] (Fig.22A, B, D).

9) Absence [0] (Fig.23C), or presence [1] (Fig.23B) of a fleshy projection at the posterior end of the genital papillae in male.

10) Absence [0] (Fig.23A), or presence [1] (Fig.23D) of a fleshy projection at the posterior end of the papilla in female.

11) Type E tubercles absent [0] (Fig.24A), or present [1] (Fig.24B) on dorsal aspect of head (Chen & Arratia 1996).

12) Tubercles on dorsal aspect of head occuring randomly [0] (Fig.24A), or unrandomly [1] (Fig.24B) (Chen & Arratia 1996).

13) Type I of tubercles absent [0], or present [1] on pectoral fin (Chen & Arratia 1996).

14) Tubercles on opercle with low density [0], or high density [1] (Chen & Arratia 1996).

15) In breeding male, each breast scale bearing less than 12 [0], or up to 16 [1] tubercles on its apical margin (Chen & Arratia 1996).

16) In females, Type G tubercle absent [0], or present [1]) on the breast scales (Chen & Arratia 1996).

17) Tubercles absent [0] (Fig.25A), or present [1] (Fig.25B) on the scales between the left and right breast scales of breeding females.

18) On anterior part of lateral body, tubercles present off from [0] (Fig.26B) or on [1] the apical margin of the scale (Fig.26C).

19) Fewer (upto six) [0] (Fig.26D), or more (upto 12) [1] (Fig.26E) tubercles present on the apical margin of each scale on caudal peduncle.

20) Two [0] (Fig.27A), or three [1] (Fig.27B) rows of tubercles on the distal portion of each pectoral fin-ray.

21) Tubercles absent [0], or present [1] on the caudal fin.

22) Presence of one horizontal stripe (*Phoxinus neogaeus*-type) [0] (Fig.22A), or two horizontal stripes (*P. erythrogaster*-type) [1] (Fig.22D), or only vertical bands (*P. phoxinus*-type) [2] (Fig.22F), or one horizontal stripe and a few verticle bands (*P. oreas*-type) [3] (Fig.22B) on the lateral body.

23) Large dark blotches absent [0] (Fig.22A), or present [1] (Fig.22B) on the dorsolateral body.

24) Few melanophores present at the isthum [0] (Fig.28A), or more melanophores present only on isthum [1] (Fig.28B), or much more melanophores present on both isthum and the anterior portion of the breast [2] (Fig.28C).

25) Melanophores absent [0] (Fig.29A), or present [1] (Fig.29B) at ventral side of caudal peduncle.

26) Pectoral fin slightly dark [0], or much darker [1] in breeding male than in nonbreeding one.

27) A dark region absent [0] (Fig.30C), or present [1] (Fig.30D) at base of dorsal fin.

28) A black patch present [0], or absent [1] at base of caudal fin.

29) Intestine *Phoxinus phoxinus*-type [0] (Fig.31A-C), or *P. eos*-type [1] (Fig.32A, C), or *P. cumberlandensis*-type [2] (Fig.31G), or *P. oreas*-type [3] (Fig.32D).

30) Gas bladder neither slender nor broad ("normal shape") [0], or very slender [1], or very broad [2].

31) Anterior chamber of gas bladder about 70% [0] (Fig.33B), or about 50% [1] (Fig.34B) or almost equal to [2] (Fig.33C) length of the anterior chamber.

32) Constriction of gas bladder very short [0] (Fig.33B), or short [1] (Fig.34C), or long [2] (Fig.34B).

33) Pneumatic duct connecting with constriction of gas bladder [0] (Fig.34B), or with anterior portion of the posterior chamber of the gas bladder [1] (Fig.34H).

34) Peritoneum silver [0], or dark [1] in color.

35) Kinethmoid short [0] (Fig.35B, D), or elongated [1] (Fig.35A, C, E).

36) Dorsal margin of kinethmoid slightly notched [0] (Fig.35D), or deeply forked [1] (Fig.35C).

37) Posterior side of kinethmoid concave [0], or not concave [1].

38) A foramen absent [0] (Fig.35A-C), or present [1] (Fig.35D, E) through anterior and posterior surfaces of kinethmoid.

39) A notch absent [0] (Fig.35B), or present [1] (Fig.35A) at ventral margin of kinethmoid.

40) Supraethmoid elongated and narrow [0] (Fig.36A), or short and broad [1] (Fig.36C).

41) Middle of lateral margin of supraethmoid convex [0] (Fig.36C, D), or not convex [1] (Fig.36A).

42) Posterior margin of supraethmoid concave [0] (Fig.36A), or unconcave [1] (Fig.36B).

43) Two small, sharp processes at laterior part of posterior margin of supraethmoid absent [0] (Fig.36A), or present [1] (Fig.36B).

44) Nasal bone narrow and elongated [0] (Fig.37E), or broad and relatively short [1] (Fig.37D).

45) Supraorbital canal on nasal bone complete [0] (Fig.37B), or interrupted [1] (Fig.37A, E).

46) Nasal bone placed over mesethmoid and lateral ethmoid [0] (Fig.37A), or over the lateral ethmoid alone [1] (Fig.37B).

47) Preethmoid small [0] (Fig.38A), or large [1] (Fig.38B).

48) Ventral side of mesethmoid elongated and narrow [0] (Fig.39A), or broad and short [1] (Fig.39B).

49) Mesethmoid bearing two [0] (Fig.39B), or one [1] (Fig.39A) conus.

50) Anterior and posterior portions of ventral side of lateral ethmoid acute [0] (Fig.39D), or blunt [1] (Fig.39C).

51) A notch absent [0] (Fig.39C), or present [1] (Fig.39D) on dorsal margin of the medial side of lateral ethmoid.

52) Posterolateral process of frontal bone short and blunt [0] (Fig.40A), or long and sharp [1] (Fig.40C).

53) Supraorbital bone slender [0] (Fig.40D), or short and broad [1] (Fig.40F).

54) Only a small portion (or none) [0] (Fig.40F), or almost half [1] (Fig.40E) of supraorbital located over lateral ethmoid.

55) Absence [0] (Fig.41A), or presence [1] (Fig.41E) of a well-developed notch at anterior and posterior margin of infraorbital bone 1.

56) Infraorbital 2 long [0] (Fig.41A), or short [1] (Fig.41B).

57) Infraorbital 3 almost equal in width for the entire bone [0] (Fig.41B), or its posterior portion broader than its anterior portion [1] (Fig.41E).

58) Anterior end of infraorbital 3 close to [0] (Fig.41H), or far from [1] (Fig.41F) the posterior end of infraorbital 2.

59) Infraorbital 4 similar to [0] (Fig.41F), or larger than [1] (Fig.41A) infraorbital 2 in size.

60) A notch absent [0] (Fig.41A), or present [1] (Fig.41E) on posterior margin of infraorbital 4.

61) Infraorbital 5 absent [0] (Fig.41B), or present [1] (Fig.41A).

62) Posterior margin of the orbital septum not extending beyond [0] (Fig.42B), or extending beyond [1] (Fig.42A) the posterior margin of the unfused portion of the orbitosphenoid.

63) A process at the ventroposterior margin of the orbital septum absent [0] (Fig.42A), or present [1] (Fig.42B).

64) A process at anterior margin of the pterosphenoid absent [0], or present [1].

65) A process on the posterior margin of pterosphenoid present [0] (Fig.43B), or absent [1] (Fig.43A).

66) A small [0] or large [1] portion of the pterosphenoid connecting with parasphenoid.

67) Medial extrascapular present [0], or absent [1] on parietal.

68) Dorsally, the lateral and medial margins of sphenoid shallowly [0] (Fig.45C), or deeply [1] (Fig.45D) concave.

69) Ventral side of sphenoid bearing four [0] (Fig.45B), or five [1] (Fig.45A), or three [2] (Fig.45D) concavities.

70) Prootic bearing a shallow [0] (Fig.46B), or a deep [1] (Fig.46C) notch on its anterior margin.

71) A process at dorsal margin present [0] (Fig.47A), or absent [1] (Fig.47B) on prootic.

72) Epioccipital rectangular [0] (Fig.46B), or triangular [1] (Fig.46A) in shape from the dorsal view.

73) A process at posterior margin of the epioccipital narrow and elongated [0] (Fig.47A), or broad and short [1] (Fig.47B).

74) Anterior concavity on the ventral aspect of epioccipital without [0] (Fig.47A), or with [1] (Fig.47C) a deeper concavity.

75) A process on the anterior margin of pterotic absent [0] (Fig.48A), or present [1] (Fig.48B).

76) Posterior process of pterotic short and blunt [0] (Fig.48A), or elongated and sharp [1] (Fig.48B).

77) Absence [0] or presence [1] of a lateral extrascapula.

78) The anterior margin of the wing-like structure of exoccipital shallowly [0] (Fig.49B), or deeply [1] (Fig.49A) concave.

79) Posterior margin of the plate-like portion of the exoccipital concave [0] (Fig.49B), or convex [1] (Fig.49A).

80) A mesial process at anterior margin of supraoccipital absent [0] (Fig.51C), or present [1] (Fig.51A).

81) Ventral side of supraoccipital bearing shallow [0] (Fig.51A), or deep [1] (Fig.51C) concavities.

82) A medial extrascapula absent [0] (Fig.44A), or present [1] (Fig.44B) on supraoccipital.

83) Vomer's posterior process short and blunt [0] (Fig.52B), or elongated and sharp [1] (Fig.52A).

84) A T-shaped ridge at dorsal side of vomer absent [0] (Fig.52A), or present [1] (Fig.52B).

85) A ridge on the dorsal side of parasphenoid poorly [0], or well [1] developed.

86) A notch at the posterior margin of ascending wing of parasphenoid large [0] (Fig.53E), or small [1] (Fig.53A).

87) Fork on the posterior end of parasphenoid broad and shallow [0] (Fig.53A), or narrow and deep [1] (Fig.53F).

88) Posterior portion of parasphenoid reaching to the posterior [0], or middle [1] portion of the dorsal part of basioccipital.

89) A notch absent [0] (Fig.55A), or present [1] (Fig.55B) at the anterior margin of basioccipital.

90) A concavity at the ventral side of the dorsal portion of basioccipital elongate and rectangular [0], or short and triangular [1].

91) Space between the anterior end of crest at the dorsal side of basioccipital broad [0] (Fig.55B), or narrow [1] (Fig.55C).

92) The crest at the dorsal side of the dorsal portion of basioccipital elongated [0] (Fig.55B), or short [1] (Fig.55A).

93) Pharyngeal pad of basioccipital poorly [0] (Fig.55A), or well [1] (Fig.55C) developed.

94) The anterior process of the pharyngeal pad of basioccipital bone present [0] (Fig.55B), or absent [1] (Fig.55A).

95) The lateral process at the anterior margin of the pharyngeal pad of basioccipital absent [0] (Fig.55A), or present [1] (Fig.13C).

96) The posterior process of basioccipital narrow [0] (Fig.55A), or broad [1] (Fig.55C).

97) The anterior process of maxilla narrow [0] (Fig.58C), or broad [1] (Fig.58C).

98) Anteromedial process of maxilla sharp [0] (Fig.58A), or blunt [1] (Fig.58B), or very small (almost absent) [2] (Fig.58C).

99) Anterior ascending process of maxilla high [0] (Fig.58E), or lower, almost absent [1] (Fig.58B).

100) The articulatory facet of maxilla formed by base of the anterior ascending process [0] (Fig.58C), or by both of the anteromedial process and the anterior ascending process [1] (Fig.58B).

101) Posterior ascending process of maxilla broad [0] (Fig.58B), or narrow [1] (Fig.58C).

102) Posterior process of maxilla extending ventroposteriorly [0] (Fig.58D), or posteriorly [1] (Fig.58B).

103) Dentary slender [0] (Fig.60C), or blunt [1] (Fig.60B).

104) Coronoid process of dentary not perpendicular to [0] (Fig.60A), or perpendicular [1] (Fig.60C) to the dorsal margin of the dentary.

105) Retroarticular short [0], or elongated [1].

106) About one third [0] (Fig.60C), or about half [1] (Fig.59A) of sesamoid bone overlapping the dentary.

107) Posterior process of anguloarticular long and blunt [0], or short and sharp [1].

108) Meckel's cartilage "normal" [0] (Fig.61A), or reduced [1] (Fig.61B) in size.

109) The anterior fork of urohyal shallow, shorter than the neck length [0] (Fig.62C), or deep, longer than the neck length [1] (Fig.62A).

110) Posterior margin of the ventral plate of urohyal concave [0], or convex [1].

111) Dorsal plate of urohyal low and elongated [0] (Fig.62A), or relatively high and short [1] (Fig.62C).

112) Anterior end of branchiostegal 1 not concave [0] (Fig.64C), or concave [1] (Fig.64B).

113) Anterior end of branchiostegal 2 sharp [0] (Fig.64B), or blunt [1] (Fig.64A).

114) Branchiostegal 3 connects with posterior ceratohyal only [0] (Fig.64A), or with both posterior and anterior ceratohyals [1] (Fig.64B).

115) Anterior end of branchiostegal 3 not concave [0] (Fig.64B), or deeply concave [1] (Fig.64D).

116) Posterior ceratohyal short-triangular [0] (Fig.65A), or long-triangular [1] (Fig.65D) in shape.

117) Anterior margin of anterior ceratohyal not concave [0] (Fig.65B), or concave [1] (Fig.65A).

118) A notch on the anterior margin of anterior ceratohyal absent [0] (Fig.65D), or present [1] (Fig.65C).

119) Hyoid foramen formed by both dorsal and ventral hypohyals [0] (Fig.66A), or by ventral hypohyal alone [1] (Fig.66B).

120) A shallow concavity absent [0], or present [1] at the dorsal side of the ventral hypohyal and the ventral side of dorsal hypohyal.

121) A concavity at the lateral margin of basihyal absent [0] (Fig.65B), or present [1] (Fig.65A).

122) Entopterygoid broad and relatively short [0] (Fig.68A), or narrow and relatively long [1] (Fig.68D).

123) Entopterygoid connecting with one half of the autopalatine [0], or with the posterior end of autopalatine only [1].

124) Ectopterygoid relatively short and broad [0], or narrow and slender [1].

125) Ectopterygoid partially overlapping [0] (Fig.68B), or not overlapping [1] (Fig.68D) the entopterygoid.

126) Dorsal margin of ectopterygoid far from [0] (Fig.68D), or close to [1] (Fig.68C) the posterior end of the autopalatine.

127) Autopalatine well [0] (Fig.68B) or poorly [1] (Fig.68D) developed.

128) Laterally, dorsal and ventral margins of autopalatine not concave [0], or concave [1].

129) A notch at posteroventral margin of quadrate absent [0] (Fig.68A), or present [1] (Fig.68C).

130) Symplectic broad [0] (Fig.68A), or slender [1] (Fig.68B).

131) The two articulating facets at posterior margin of metapterygoid for the hyomandibula small [0], or large [1].

132) Notch on the dorsal margin of metapterygoid deep [0], or shallow [1].

133) Processus basalis (basal process) of metapterygoid narrow and high [0] (Fig.67C), or broad and low [1] (Fig.67A).

134) Hyomandibula broad and relatively short [0], or narrow and relatively long [1].

135) A notch at the ventroanterior margin of hyomandibula absent [0] (Fig.69A), or present [1] (Fig.69B).

136) A posterior notch at ventroposterior margin of hyomandibula absent [0] (Fig.69A), or present [1] (Fig.69C).

137) A small [0] (Fig.69A), or large [1] (Fig.69C) cartilage present at ventral side of hyomandibula.

138) Opercle short and broad [0], or long and narrow [1].

139) Dorsal margin of opercle straight [0], or shallowly concave [1].

140) Anterodorsal process of opercle broad and round [0], or narrow and sharp [1].

141) Anterior margin of subopercle concave [0], or straight [1].

142) Posterior margin of pharyngobranchial 1 not forked [0] (Fig.72A), or forked [1] (Fig.72E).

143) Pharyngobranchial 2+3 uncrescent [0] (Fig.72A), or crescent [1] (Fig.72B) in shape.

144) Pharyngobranchial 4 absent [0] (Fig.74A), or present as a cartilage [1] (Fig.74E).

145) Dorsal portion of epibranchial 1 not constricted [0] (Fig.72A), or constricted [1] (Fig.72E).

146) Dorsal portion of epibranchial 2 slightly constricted [0] (Fig.72C), or well-constricted [1] (Fig.72D).

147) Ventral margin of epibranchial 2 not concave [0] (Fig.72A), or deeply concave [1] (Fig.72D).

148) Posterior process of the forked portion of epibranchial 3 much shorter than [0] (Fig.72A), or almost equal to [1] (Fig.72C) the anterior process of the structure in length.

149) A process absent [0] (Fig.72A), or present [1] (Fig.72C) on the lateral side of epibranchial 3.

150) Ventral margin of epibranchial 4 straight [0] (Fig.72D), or deeply concave [1] (Fig.72A).

151) Dorsal margin of epibranchial 4 not concave [0] (Fig.72B), or deeply concave [1] (Fig.72A).

152) Posterior margin of epibranchial 4 shallowly concave [0], or deeply concave [1].

153) A process absent [0] (Fig.72A), or present [1] (Fig.72B) at the lateral side of epibranchial 4.

154) Hypobranchial 3 short [0] (Fig.73B), or elongated [1] (Fig.73A).

155) Basibranchial 1 short bar-shaped [0] (Fig.73A) or wedge-shaped [1] (Fig.73F).

156) Basibranchial 2 bar-shaped [0] (Fig.73A), or wedge-shaped [1] (Fig.73D).

157) Basibranchial 3 similar to [0] (Fig.73B), or much longer than [1] (Fig.73A) basibranchial 2 in size.

158) A cartilage at the posterior end of basibranchial 3 very small [0] (Fig.73A), or elongated [1] (Fig.73D).

159) Posterior angle of the pharyngeal bone large [0], or small [1].

160) A small flat plate-like structure with two small processes absent [0], or present [1] at the posterior edentulous process of the pharyngeal bone.

161) Anterior edentulous process of pharyngeal bone curved [0], or straight [1].

162) A notch absent [0], or present [1] at the anterior limb's tip of pharyngeal bone.

163) Pitted surface of pharyngeal bone bearing large and small pits [0] or large pits only [1].

164) Pharyngeal teeth on pharyngeal bone in two rows [0], or one row [1].

165) Transverse process 1 located at middle [0] (Fig.75A), or anterior portion [1] (Fig.75B) of the centrum of the vertebra 1.

166) Transverse process of vertebra 1 long [0] (Fig.75A), or short [1] (Fig.75B).

167) Neural arch 2 not bearing [0] (Fig.76A), or bearing [1] (Fig.76B) an ascending process.

168) Anterior process of neural arch 3 short and broad [0] (Fig.77B), or long and narrow [1] (Fig.77A).

169) A shallow notch absent [0] (Fig.78B), or present [1] (Fig.78A) at medial side of rib 4.

170) Os suspensorium narrow [0] (Fig.78C), or broad [1] (Fig.78B).

171) A notch absent [0] (Fig.78B), or present [1] (Fig.78A) at the medial edge of os suspensorium.

172) The space between the left and right os suspensorium extending to the ventral margin [0] (Fig.78A), or to the middle [1] (Fig.78C) of os suspensorium.

173) Notch at the anterior margin of neural arch 4 deep [0], or shallow [1].

174) Space between the neural arch 4 and neural arch 3 extending to the ventral portion [0] (Fig.76A), or to the middle [1] (Fig.76B) of the anterior margin of neural arch 4.

175) A process absent [0] (Fig.77B), or present [1] (Fig. 77A) at the dorsoposterior margin of neural spine 4.

176) Supraneural 3 narrow and tall [0] (Fig.77A), or broad and short [1] (Fig.77B).

177) Grooved portion of supraneural 3 broad [0] (Fig.77B), or narrow [1] (Fig.77A).

178) The entire dorsal margin of supraneural 3 grooved [0] (Fig.76A), or only the posterior part of the margin grooved [1] (Fig.76C).

179) Dorsal margin of the intercalarium shallowly [0] (Fig.79C), or deeply [1] (Fig.79B) concave.

180) Main part of the intercalarium short [0], or slender [1].

181) Lateral spine of the intercalarium short [0] (Fig.79B), or elongate [1] (Fig.79A).

182) Posterior ramus of the tripus broad and short [0], or elongated and slender [1].

183) Supraneural 4 small [0] (Fig.77C), or large [1] (Fig.77B).

184) Supraneural 4 a single bone [0] (Fig.76A), or pieced into two parts [1] (Fig.76B).

185) Ventral portion of the posttemporal not expanded [0] (Fig.82A), or expanded [1] (Fig.82C).

186) Posttemporal not overlapping [0] (Fig.82B), or overlapping [1] (Fig.82C) pterotic.

187) Dorsal portion of supracleithrum slightly narrower [0] (Fig.82C), or much narrower [1] (Fig.82A) than the ventral portion of the bone.

188) Notch at posterior margin of the horizontal branch of cleithrum shallow [0] (Fig.83B), or deep [1] (Fig.83C).

189) Ventral margin of the ascending process of cleithrum slope [0] (Fig.83B), or almost vertical [1] (Fig.83C).

190) Anterior portion of the slender part of coracoid not narrower [0] (Fig.85B), or narrower [1] (Fig.85E) than the posterior portion of the slender part.

191) A forked structure absent [0] (Fig.85B), or present [1] (Fig.85F) at the broad part of coracoid.

192) Cleithral end of mesocoracoid blunt [0] or sharp [1].

193) Cleithral process of mesocoracoid curved [0], or straight [1].

194) A notch absent (0) (Fig.84E), or present (1) (Fig.84G) at cleithral process of mesocoracoid.

195) Coracoidal end of mesocoracoid expanding [0] (Fig.84E), or not expanding [1] (Fig.84F).

196) Articular facets on the lateral side of radial 1 of the pectoral fin low [0] (Fig.87A), or high [1] (Fig.87E).

197) Pectoral radial 2 slender [0] (Fig.87E), or triangular [1] (Fig.87A).

198) A process at the medial margin of pectoral radial 2 absent [0] (Fig.87C), or present [1] (Fig.87E).

199) A process absent [0] (Fig.87B), or present [1] (Fig.87A) on pectoral radial 3.

200) Segments of the first pectoral fin ray high and narrow [0] (Fig.88A), or short and broad [1] (Fig.88B).

201) Anterior fork of pelvic basipterygium deep [0] (Fig.89D), or shallow [1] (Fig.89C).

202) Medial process of pelvic basipterygium broad and forked [0] (Fig.89A), or narrow and unforked [1] (Fig.89B).

203) Ischiac process of pelvic basipterygium narrow and elongated triangular [0] (Fig.89G), or broad and short triangular [1] (Fig.89C) in shape.

204) A cartilage at the posterior end of the ischiac process of pelvic basipterygium absent [0] (Fig.89B), or present [1] (Fig.89D).

205) Pelvic radial 4 triangular [0] (Fig.89B), or bar-shaped [1] (Fig.89D).

206) Proximal part of the first dorsal pterygiophore broad [0] (Fig.90A), or slender [1] (Fig.90F).

207) Anterior process of the proximal part of dorsal fin's first pterygiophore much shorter than [0] (Fig.90A), or equal to [1] (Fig.90C) its posterior process in length.

208) Proximal part of the first anal pterygiophore unforked [0] (Fig.91A), or forked [1] (Fig.91B).

209) Epural short [0] (Fig.95B), or elongated [1] (Fig.92A).

210) Hypural 6 present [0] (Fig.95A), or absent [1] (Fig.92C).

Appendix IV

List of abbreviations used in figures and text

AAP	Anterior ascending process of maxilla
AC	Anterior chamber of gas bladder
ACH	Anterior ceratohyal
ACO	Anterior conus of mesethmoid
ADP	Anterior dorsal vertebral postzygapophysis
AEP	Anterior edentulous process of the pharyngeal bone
AF	Anal fin
AFMEP	Articular surface of metapterygoid for hyomandibular
AFT	Articular surface of maxilla
AL	Anterior limb of pharyngeal bone
AMP	Anteromedial process of maxilla
ANA	Anterior nasal opening
ANF	Anterior fork of urohyal
ANP	Anterior process of maxilla
ANT	Anterior
ANTPB	Anterior process of basioccipital
APA	Apical radial of scale
APAL	Autopalatine
APORS	Anterior process of orbital septum
APTG	Anal pterygiophore
AR	Anterior ramus of tripus
ART	Anguloarticular
AW	Ascending wing of parasphenoid
AX	Axis of olfactory organ
BAR	Barbel
BB	Basibranchial
BH	Basihyal
BO	Basioccipital
BPB	Body portion of exoccipital
BPC	Broader part of coracoid bone
BR	Branchiostegal ray
BRA	Basal radial of scale
BST	Breast scale with tubercles
CA	Cartilage
CAB	Cartilage at posterior end of ischiac process of basipterygium
CB	Ceratobranchial
CEB	Canal formed by exoccipital and basioccipital
CEM	Cleithral end of mesocoracoid
CL	Cleithrum
CLA	Claustrum
CO	Cavity
COEM	Coracoidal end of mesocoracoid
CON	Constriction of gas bladder
COR	Coracoid
CP	Coronoid process
CPM	Cleithral process of mesocoracoid
CR	Crest
DE	Dentary
DENT	Dentigerous surface of pharyngeal bone
DLPI	Dorsolateral process of intercalarium
DMPI	Dorsomedial process of intercalarium
DPB	Dorsal portion of basioccipital
DPU	Dorsal plate of urohyal
EB	Epibranchial
ECP	Ectopterygoid
ENP	Entopterygoid
EOC	Exoccipital
EP	Epural
EPOC	Epioccipital
EYE	Eye
FIC	Carotid foramen
FOM	Foramen
FR	Frontal
FV	Trigeminal foramen
FVII	Facial foramen
GP	Genital papilla
GS	Gill cleft
H	Hypural
HA	Haemal arch
HB	Hypobranchial
HF	Hyoid foramen
HH	Hypohyal
HLS	Horizontal lateral strip on the flank
HS	Haemal spine
ICA	Intercalarium
IH	Interhyal
IO	Infraorbital bone
IOP	Interopercle
IP	Ischiac project of basipterygium
LB	Lateral pelvic plate of basipterygium
LE	Lateral ethmoid
LES	Lateral extrascapula
Lig	Ligament

LL	Body lateral line
LOF	Lateral occipital foramen
LPS	Lateroposterior process of supraethmoid
LRIB	Last rib
MAC	Mandibular canal
MAP	Main part of maxilla
MAR	Main row of pharyngeal teeth
MB	Medial pelvic plate of basipterygium of the pelvic girdle
MC	Meckel's cartilage
MCO	Mesocoracoid
ME	Mesethmoid
MEP	Metapterygoid
MES	Medial extrascapula
MIR	Minor row of pharyngeal teeth
MLP	Melanophore
MP	Medial process of basipterygium
MPI	Main part of intercalarium
MR	Medial ramus of tripus
N	Nasal bone
NA	Neural arch
NE	Neck portion of urohyal
NO	Notch
NOR	North
NPSCA	Nasal portion of supraorbital sensory canal
NS	Neural spine
OP	Opercle
ORS	Orbitosphenoid
OS	Os suspensorium
OSE	Orbital septum
OTC	Otic canal of cephalic lateral line
PA	Parietal
PAN	Posterior angle of pharyngeal bone
PAP	Posterior ascending process of maxilla
PAS	Parasphenoid
PC	Posterior chamber of gas bladder
PCA	Preopercular sensory canal
PCH	Posterior ceratohyal
PCO	Posterior conus of mesethmoid
PD	Pneumatic duct
PDP	Posterior dorsal vertebral postzygopophysis
PE	Planum ethmoidale
PEP	Posterior edentulous process of pharyngeal bone
PF	Pitted surface of pharyngeal bone
PH	Parhypural
PHB	Pharyngobranchial
PIT	Pit of pharyngeal bones
PLE	Plate-like structure of exoccipital
PLF	Pelvic fin
PLOO	Primary lamella of olfactory organ
PLPFR	Posterolateral process of frontal
PMC	Preoperculomandibular canal
PNA	Posterior nasal opening
POP	Preopercle
POPM	Posterior process of maxilla
PP	Posterior projection of genital papilla
PPBO	Posterior process of basioccipital
PPD	Pharyngeal pad of the basioccipital
PR	Posterior ramus of tripus
PRB	Processus basalis of the metapterygoid
PRE	Preethmoid
PRML	Processus metapterygoideus lateralis of metapterygoid
PRO	Prootic
PT	Pharyngeal tooth
PTC	Postcleithrum
PTF	Pectoral fin
PTG	Anal pterygiophore
PTO	Pterotic
PTS	Pterosphenoid
PTT	Posttemporal
PU	Preural centrum
PVP	Posterior ventral postzygopophysis of vertebra
QA	Quadrate
RA	Retroarticular
RAD	Radial
RIB	Rib
RPF	Pectoral fin ray
SB	Sesamoid bone (sesamoid articular)
SC	Scale
SCA	Scapula
SCAP	Scaphium
SCL	Supracleithrum
SE	Supraethmoid
SF	Skin fold
SN	Supraneural bone
SO	Supraorbital
SOC	Supraoccipital
SOCA	Supraorbital canal
SOP	Subopercle

SPC	Slender part of coracoid
SUCA	Supratemporal canal of cephalic lateral line
SY	Symplectic
TPV	Transverse process of vertebra
TRP	Tripus
TU	Tubercle
U	Urostyle
V	Vertebra
VLS	Vertical lateral strip of the flank
VO	Vomer
VPU	Ventral plate of urohyal
WSE	Wing-like structure of exoccipital

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