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INTRODUCTION

The flathead chub, *Hybopsis gracilis* (Richardson), occurs in the Plains Region of Canada and the United States, in four major drainage systems: Mackenzie River, which discharges into the Arctic Ocean; Saskatchewan River, which discharges into Hudson Bay via Nelson River; and Missouri-Mississippi System and Rio Grande, both draining into the Gulf of Mexico. Each of these systems is occupied in part only. In the Mackenzie Basin, *H. gracilis* has been reported as far north as Fort Good Hope (Walters, 1955:347). Flathead chubs occur in the Saskatchewan Basin from Alberta eastward to Lake Winnipeg, Manitoba, but have not been found in other streams that flow into Lake Winnipeg (Red River, Brokenhead River and Whitemouth River) nor in Nelson River downstream from Lake Winnipeg. In the Missouri Basin the species occurs more or less continuously from the high plains adjacent to the Rocky Mountains in Montana and Wyoming down the mainstream of the Missouri River to its mouth, and down the mainstream of the Mississippi River as far as Barfield, Arkansas, but not to the Gulf. The species probably attains its [pg 326] greatest abundance in the Missouri Basin, but it is scarce or absent in tributaries north and east of the Missouri mainstream, in the South Platte Basin, and in the central part of the Platte River in Nebraska. The flathead chub is unknown in the Mississippi Basin above the mouth of the Missouri River, and in the Ohio River Basin above its mouth. In the Arkansas River Basin, records are restricted to (1) the headwaters and tributaries of the Arkansas River from eastern Colorado downstream as far as Garden City, Kansas, (2) the Cimarron River at Kenton, Cimarron County, Oklahoma, and (3) the South Canadian River and tributaries from northeastern New Mexico eastward as far as Norman, McClain County, Oklahoma, but rarely there. Thus, the range in the Arkansas Basin seems to consist of three isolated segments. Likewise, isolated populations exist in the Rio Grande System, where flathead chubs are confined to the upper parts of the Rio Grande and Pecos basins, above the confluence of the Rio Grande and Pecos Rivers. Records resulting from introductions have been reported for the Gila River by Koster (1957:62) and from the Snake River, Wyoming, by Simon (1946:72).

Six names apply to the flathead chub, the earliest of which is *Cyprinus gracilis* Richardson (1836:120). Other names have sometimes been accepted as applicable to valid species and/or subspecies, but usage, diagnoses, and stated ranges have been confusingly inconsistent. For most of the past 100 years, *Platygobio* Gill has been recognized as the appropriate generic name for the flathead chub, but Bailey (1951:192) places *Platygobio* and other nominal genera of barbeled minnows having short guts, protractile premaxillae, and four teeth (primary row) in the single genus *Hybopsis* (Agassiz, 1854). Strangely, the orthotype of *Hybopsis*, *H. gracilis* Agassiz, is a junior synonym of *H. amblops* (Rafinesque) (Hubbs and Ortenburger, 1929b:66) and is a younger name than *C. gracilis* Richardson.

The purpose of this paper is to redescribe the species and to make known its pattern of geographic variation. Natural history will also be considered, as will habitat, food habits, and breeding season.

METHODS, MATERIALS AND ACKNOWLEDGMENTS

Ten meristic characters and seventeen measurements of body-parts (the latter expressed as proportions of standard length) have been analyzed. They are: number of rays in the dorsal, anal, caudal, pectoral and pelvic fins; number of scales in the lateral line, before the dorsal fin, around the body and around the caudal peduncle; number of vertebrae; body-depth, depth of caudal peduncle, length of caudal peduncle, predorsal length, length of depressed anal and dorsal fins, length of pectoral and pelvic fins, head-length, head-depth, head-width, snout-length, postorbital length of head, length of [pg 327] orbit, interorbital width, length of upper jaw and width of gape.

Counts and measurements were made as described by Hubbs and Lagler (1958), with the exception of scales before the dorsal fin, which were counted as the number of vertical scale-rows between the upper margin of the opercular cleft and the origin of the dorsal fin. Vertebral counts, made from roentgenograms, excluded vertebrae in the Weberian complex (presumably always four) but included the hypural vertebra.

Counts and measurements were made on series (usually ten fish) from localities throughout the range. To minimize effects of allometric growth, the fish were divided into several length-groups prior to analysis of proportional measurements: 30-50mm, 50-70mm, 70-100mm, 100-150mm, 150-200mm and 200mm standard length and over. The majority of specimens examined were 70-100mm in standard length.

Specimens were obtained from the following institutions: University of Alberta (abbreviated AU in the text); Museum of Zoology, University of Michigan (UMMZ); University of Missouri (UM); Montana State College (MSC); University of Oklahoma Museum of Zoology (UOMZ); University of Saskatchewan; Royal Ontario Museum, Division of Zoology, Toronto (ROMZ); University of Wyoming (WU); Museum of Natural History, University of Kansas (KU). Specimens examined are listed in the accounts of the subspecies.

We are grateful to D. A. Boag, Reeve M. Bailey, Arthur L. Witt, C. J. D. Brown, Carl Riggs, F. M. Atton, W. B. Scott, and George Baxter, all staff-members of the institutions listed in the immediately preceding paragraph, for placing specimens at our disposal. Mr. William Peters analyzed the contents of stomachs of specimens that were used for study of the food habits. Mr. Artie L. Metcalf assisted in collecting specimens. Drs. Kenneth B. Armitage and E. Raymond Hall offered valued suggestions in connection with the preparation of the manuscript.

DESCRIPTION OF THE SPECIES

Hybopsis gracilis (Richardson)

Flathead Chub

(Synonymy under accounts of subspecies)

Description.--Pharyngeal teeth 2,4-4,2, hooked; dorsal fin of moderate size, falcate, first principal ray longest, extending beyond posterior rays in depressed fin, its origin usually slightly in front of insertion of pelvic fin, approximately equidistant from tip of snout and base of caudal fin, rays 8, rarely 9; pectoral fin strongly falcate, rays 14-20, usually 16-18; pelvic rays 8, rarely 9; anal fin falcate, rays 8, rarely 9; caudal rays 19, rarely 20.

Body slightly compressed, nearly terete; head-length 23.1-28.8 per cent of standard length; head broad and flattened, snout subconical, premaxillae protractile, upper lip not medially expanded; mouth subterminal, nearly horizontal, large; a single pair of terminal maxillary barbels; orbit usually 5-7 per cent of standard length; lateral line slightly decurved; intestine short, peritoneum silvery.

Color brown or olivaceous dorsally, silver or creamy white ventrally, without distinctive markings; dusky lateral band evident in preserved specimens.

Taste-buds present on membrane between first and second principal rays of all fins, [pg 328] and on first to sixth interradial membranes of pectoral fin. On the caudal fin, taste buds between first and second principal rays of upper and lower lobes, though present, are less well developed than on other fins. Moore (1950:88) states that taste buds are numerous on the barbels, cheeks, lips, chin, snout, opercles and branchial membranes, and are present in decreasing numbers over the body.

Nuptial tubercles of male minute and densely scattered over top of head and snout; usually present on pectoral rays 1-8, weak when present on rays beyond the eighth, never found beyond the eleventh ray; minute tubercles usually found on dorsal, pelvic and anal fins, rarely on lower scales of caudal peduncle; predorsal scales have a fine peripheral row of tubercles.

Hybopsis gracilis gracilis (Richardson)

(Plate 22)

Cyprinus (Leuciscus) gracilis Richardson, 1836:120 and Pl. 78 (original description; Saskatchewan R. at Carlton House).

Coregonus angusticeps Cuvier and Valenciennes, 1848:534 (original description; Saskatchewan R.).

Pogonichthys communis Girard, 1856:188 (in part; original description); Girard, 1858:247 and plate 55 (in part; characters; synonymy); Suckley, 1860:361 (Milk R.); Cope, 1879:440 (Fort Benton, Mo. R.; Judith R.).

Platygobio gracilis, Jordan and Gilbert, 1882:219 (in part; characters; synonymy); Graham, 1885:74 (Kansas R.; synonymy); Jordan, 1885:29 (records); Jordan and Meek, 1886:13 (Mo. R., St. Joseph, Mo.); Meek, 1892:245 (characters; Mo. R., Sioux City, Iowa); Eigenmann, 1895:111 (Craig; Poplar; Brandon; Medicine Hat); Meek, 1895:137 (Platte R., Fremont, Neb.); Evermann and Cox, 1896:412 (in part; habitat; synonymy); Jordan and Evermann, 1896:326 (in part; characters; synonymy); Thompson, 1898:214 (Brandon; Saskatchewan R.); Evermann and Goldsborough, 1907:98 (records from Canada); Forbes and Richardson, 1920:170 (characters; habitat; synonymy; records from Illinois; but Fig. 45 is *Hybopsis meeki* Jordan and Evermann, not *H. gracilis*); Hankinson, 1929:446 (records from North Dakota); Jordan, 1929:76 (in part; characters); Jordan, Evermann and Clark, 1930:136 (in part; synonymy); Churchill and Over, 1933:45 (characters; food; habitat; spawning; records from South Dakota); O'Donnel, 1935:481 (Ohio R., Cairo, Ill.; Miss. R., Chester, Ill.); Hinks, 1943:57 (records from Canada); Clemens, *et al.*, 1947:17 (records from Saskatchewan); Dymond, 1947:19 (distribution in Canada); Rawson, 1951:208 (Great Slave Lake; Mackenzie R.); Shoemaker, Pickering and Durham, 1951:84 Miss. R., Cates, Tenn.; Miss. R., between Hickman and Barfield, Ark.); Wynne-Edwards, 1952:18 (distribution in Canada); Miller and Paetz, 1953:47 (Peace R. at town of Peace River); Walters, 1955:347 (distribution in Canada; dispersal into Canada); Keleher, 1956:265 (Saskatchewan R., Manitoba); Lindsey, 1956:771 (distribution in Canada); Keleher and Kooyman, 1957:110 (Kelsey Lake, Manitoba); Lindsey, 1957:657 (Laird and Peace drainages, British Columbia); Scott, 1958:16 (distribution in Canada); Slastenenko, 1958:7 (distribution in Canada).

Platygobio pallidus Jordan and Gilbert, 1882:220 (original description; Ohio R., Cairo, Ill.); Jordan and Evermann, 1896:326 (characters; synonymy; Ohio R., Cairo, Ill.); Jordan, Evermann and Clark, 1930:136 (Ohio R., Cairo, Ill.; synonymy).

Platygobio gracilis communis, Simon, 1946:71 (in part; characters; food; habitat; spawning); Moore, 1950:87 (habitat; sense organs).

Hybopsis gracilis communis, Bailey, 1951:192 (record from Iowa; key); Harlan and Speaker, 1951:75 (characters; distribution in Iowa); Hubbs, 1951:9 (habitat; Miss. R.); Harrison and Speaker, 1954:516 (habitat); Personius and Eddy, 1955:42 (habitat; Little Mo. R.). [pg 329]

Hybopsis gracilis, Cleary, 1956:271 (record from Iowa; distributional map); Bailey, 1956:332 (record from Iowa; key); Harlan and Speaker, 1956:90 (characters; distribution in Iowa); Eddy, 1957:111 (in part; characters; key); Moore, 1957:110 (in part; key); Underhill, 1959:100 (Vermillion R., South Dakota).

Diagnosis.--Post-Weberian vertebrae 40-42, usually 41-42; lateral line scales 50-56; pectoral rays 15-20, usually 17 or more; head-depth 12.3-15.1 per cent of standard length, usually 14.7 per cent or less. See Figs. 1 and 2.

Other characters.--Circumference scale-rows 31-42; predorsal scale-rows 20-29; size large, as much as 246 mm standard length (see Fig. 1 of Pl. 24); head-length 23.4-27.4 per cent of standard length, usually 25.5 per cent or less; postorbital length of head 10.9-13.9 per cent of standard length, usually 12.5 per cent or less; predorsal length 46.0-51.7 per cent of standard length; orbit 5.1-6.8 per cent of standard length; prepelvic length 46.6-52.2 per cent of standard length; caudal peduncle length 17.2-22.1 per cent of standard length.

Range (Plate 21).--Mackenzie Basin south from Fort Good Hope; Saskatchewan Basin east to Lake Winnipeg; mainstream of Missouri River and Mississippi River south to Barfield, Arkansas; intergrading with *H. g. gulonella* in upper Missouri Basin and lower parts of major tributaries to Missouri River in Nebraska and Kansas.

Specimens examined.--Below are listed museum numbers, number of specimens (in parentheses), localities, and year of collection. Collections marked with asterisk (*) are intergrades more closely resembling *H. g. gracilis* than *H. g. gulonella*. Records from literature are cited in the synonymy.

Alberta: UA (6), Milk R. at town of Milk River, 1950; UA (3), Athabasca R. at Fort McMurray, 1955; UA (1), Red Deer R. at Steveville, 1952; UA (2), Peace R. at town of Peace River, 1952; UA (11), Peace R. at Dunvegan, 1956; UA (2), Simonette R. tributary to Smoky R., date unknown; ROMZ 17704 (1), Milk R. W town of Milk River, 1955.

Arkansas: UMMZ 128573 (5), Mississippi Co., Mississippi R., 1939.

Illinois: UMMZ 134799 (146), Mississippi R. at Grand Tower, 1936; UMMZ 147045 (8), Mississippi R. at Cairo, 1944.

Kansas: KU 1234 (173), Leavenworth Co., backwater of Missouri R. near Corral Cr., 1940; * KU 1814 (1), Douglas Co., floodpool of Kansas R., below Lakeview, 1951; * KU 1825 (1), Douglas Co., floodpool of Kansas R., 1951; * KU 1841 (56), Douglas Co., Kansas R. at Lawrence, 1951; * KU 1898 (6), Douglas Co., floodpool of Kansas R., 1951; * KU 1911 (5), Douglas Co., floodpool of Kansas R., 1951; * KU 1928 (2), Jefferson Co., floodpool of Kansas R., 1951; KU 3850 (30), Atchison Co., Missouri R., 1957; * KU 4377 (2), Douglas Co., Kansas R. at Lawrence, 1958; * KU 4655 (2), Douglas Co., Kansas R. at Lawrence, 1959.

Manitoba: ROMZ 13834 (1), Kelsey Lake, 25 miles east of the Pas, no date; ROMZ 14500 (25), Saskatchewan R. at the Pas, 1947; ROMZ 16325 (1), Lake Winnipeg, no date.

Missouri: UMMZ 147126 (130), Mississippi R. at Cliff Cave, 1944.

Montana: * MSC 1878 (36), Carbon Co., Elbow Cr., 1957; * MSC 1943 (11), Phillips Co., Frenchman Cr., 1957; * MSC 2021 (10), Pondora Co., Marias R., 1955; * MSC 2022 (4), Lewis and Clark Co., Missouri R. below Holter Dam, 1948; * MSC 2052 (6), Gallatin Co., Missouri R. near Trident, 1948; * MSC 3074 (3), Custer Co., Hardy Reservoir, 1952; UMMZ 94146 (34), near mouth of Powder R., 1926. [pg 330]

Nebraska: * KU 4158 (9), Holt Co., Niobrara R. 6 mi. N Midway, 1958; * UM (field no. 59-81) (56), Butler Co.-Colfax Co. line, Platte R. 1.5 mi. S Schuyler, 1959; * UM (field no. 59-74) (5), Dodge Co., Platte R. 1 mi. S North Bend, 1959; UMMZ 134826 (46), Otoe Co., Missouri R. 1.5 mi. E Minersville, 1940; UMMZ 134799 (67), Cass Co., Missouri R., 1940; UMMZ 135341 (43), Knox Co., Missouri R. 2 mi. NE Niobrara, 1940; UMMZ 135818 (95), Thurston Co., Missouri R. NE Macy, 1941.

Northwest Territory: ROMZ 13627 (1), Great Slave Lake, no date; ROMZ 13628 (1), Great Slave Lake, no date.

Saskatchewan: * ROMZ 3885 (2), Sucker Cr., trib. Cypress Lake, 1927; ROMZ 14368 (2), South Saskatchewan R. at Yorath Island, 1941; ROMZ 16620 (5), South Saskatchewan R. at Saskatoon, 1953; KU 5126 (5), South Saskatchewan R. at Birson Ferry, 1957; KU 5127 (3), South Saskatchewan R. at Leader, 1957; KU 5128 (2), North Saskatchewan R. at Cecil Ferry, 1957; KU 5129 (1), South Saskatchewan R. at Clarkboro Ferry, 1957.

South Dakota: * KU 4961 (9), Haakon Co., Bad R. at Midland, 1959; * KU 4963 (17), Washabaugh Co., White R. 6 mi. SW Belvidere, 1959; * UMMZ 120362 (168), White R. 6.5 mi. S Kadoka, 1934; * UMMZ 127484 (11), Todd Co., Little White R., 1934; UMMZ 127488 (29), Charles Mix Co., Missouri R., 1934; * UMMZ 127678 (32), Cheyenne R., E Wasta, 1939; UMMZ 166762 (21), Hughes Co., Missouri R. 3 mi. NE Pierre, 1952; * UMMZ 166803 (91), Harding Co., Little Missouri R. at Camp Crook, 1952; UMMZ 166845 (121), Carson Co.-Walworth Co. line, Missouri R. 2.5 mi. N Mobridge, 1952; UMMZ 166985 (61), Yankton Co., Missouri R. at Yankton, 1952.

Wyoming: * WU 2073 (6), Washakie Co., Big Horn R. at Worland, 1956.

Hybopsis gracilis gulonella (Cope)

(Plate 23)

Pogonichthys communis Girard, 1856:188 (in part; original description); Girard, 1858:247 (in part; characters; synonymy); Cope and Yarrow, 1875:653 (characters; Pueblo, Colo.).

Pogonichthys (Platygobio) gulonellus Cope, 1864:277 (original description; near Bridger's Pass, Wyo.).

Platygobio gulonellus Cope, 1865:85 ("Platte R., near Fort Riley" [Fort Riley is on Kansas R., not Platte R.; Cope's specimens probably are from Platte drainage, on basis of known distributions of other species reported]).

Ceratichthys physignathus Cope and Yarrow, 1875:651 (original description; Arkansas R., Pueblo, Colo.).

Platygobio communis, Gill, 1876:408 (characters; Platte Valley; Green River, Utah [the latter probably erroneous]).

Couesius physignathus, Jordan and Gilbert, 1882:219 (characters; synonymy; Arkansas R., Pueblo, Colo.); Jordan, 1885:29 (records).

Platygobio gracilis, Jordan and Gilbert, 1882:219 (in part; characters; synonymy); Cragin, 1885:109 (Garden City, Kans.); Gilbert, 1885:98 (Garden City, Kans.); Jordan, 1885:29 (records); Evermann and Cox, 1896:412 (in part; habitat; synonymy); Jordan and Evermann, 1896:326 (in part; characters; synonymy); Ortenburger and Hubbs, 1927:125 (Canadian R., Norman, Okla.); Hubbs, 1927:75 (parasites; teratology; records from New Mexico); Hubbs and Ortenburger, 1929a:28 (S. Canadian R., Durham, Okla.); Jordan, 1929:76 (in part; characters); Jordan, Evermann and Clark, 1930:136 (in part; synonymy).

Platygobio physignathus, Jordan and Evermann, 1896:325 (characters; synonymy; records from upper Arkansas R.); Ellis, 1914:62 (characters; synonymy; records from Colorado); Cockerell, 1927:123 (distribution in Colorado); Jordan, Evermann and Clark, 1930:136 (synonymy; records from upper Arkansas R.). [pg 331]

Platygobio gracilis communis, Simon, 1946:71 (in part; characters; food; habitat; spawning).

Platygobio gracilis gulonellus, Simon, 1946:72 (characters; records from Wyoming; Arkansas R.).

Platygobio gracilis: communis × *gulonellus*, Simon, 1946:92 (North Platte R., Neb.-Wyo. line).

Platygobio gracilis physignathus, Moore, 1950:87 (habitat; sense organs).

Hybopsis gracilis communis, Beckman, 1952:50 (characters; food; habitat); Cross, Dalquest and Lewis, 1955:222 (records from Texas).

Hybopsis gracilis physignathus, Beckman, 1952:50 (characters; habitat).

Hybopsis gracilis, Eddy, 1957:111 (in part; characters; key); Koster, 1957:61 (characters; habitat; spawning; food); Moore, 1957:110 (in part; key); Smith, 1958:177 (fossil record; Doby Springs, Okla.).

Diagnosis.--Post-Weberian vertebrae 36-38, rarely 39; lateral line scales 42-54, usually less than 50; pectoral rays 14-19, usually fewer than 17; head-depth 13.5-18.0 per cent of standard length, usually 14.8 per cent or more. See Figures 1 and 2.

Other characters.--Circumference scale-rows 30-40, slightly fewer than in *H. g. gracilis*; predorsal scale-rows 17-27, somewhat fewer than in specimens from Canada, but much the same as specimens from the Missouri-Mississippi system; size small, rarely as much as 130 mm standard length (Fig. 1 of Pl. 24); head-length 24.0-28.0 per cent of standard length, usually more than 25.5 per cent; postorbital length of head 11.2-14.4 per cent of standard length, usually more than 12.5 per cent (both characters illustrate the larger head of *H. g. gulonella*); predorsal length 46.4-52.7 per cent of standard length, longer than in the other subspecies; orbit 5.0-6.6 per cent of standard length; prepelvic length 47.4-53.7 per cent of standard length, longer than in *H. g. gracilis*; caudal peduncle length 17.1-22.7 per cent of standard length, essentially the same in both subspecies.

The label on types of this subspecies, in the Academy of Natural Sciences of Philadelphia, states merely "near Bridger's Pass, Wyo., Expedition of 1856, Dr. W. A. Hammond" (letter from Dr. James Böhlke to Cross, dated Jan. 27, 1960). Dr. Hammond was a surgeon who also collected scientific specimens, assigned to an expedition under the command of Lt. F. T. Bryant. Bryant's log is recorded in the Proceedings of the 35th Congress (1858:455-481). The site at which these specimens were taken cannot be ascertained from the log, but study of it is helpful in indicating the probable locations.

The expedition left Fort Riley on June 21, 1856, on the following route: up Republican River; across to Fort Kearney on Platte River; west along Platte River to S. Platte River; up S. Platte River to Pole (Lodgepole) Creek; Pine-Bluffs (Neb.-Wyo. line); across East Fork to West Fork of Laramie River; Cooper's Creek; West Fork of Medicine Bow; Pass Creek and down canyon of Pass Creek; across N. Platte River; up Sage Creek; on August 15, camped on Muddy Creek, tributary to Green River (first record of fish, trout); back to Sage Creek; August 19-21, camped on island in North Platte River; to Pass Creek; Elk Creek; west branch of Medicine Bow; Aspen Creek; West Fork of Laramie River; August 29, to East Laramie River where a large supply of fish was caught; tributary of Cache la Poudre then downstream to mouth of this river; down South Platte River past mouth of Crow Creek and Beaver Creek; left South Platte River 14 miles below mouth of Beaver Creek, toward Republican River; down Rock Creek to Arikaree; down Arikaree to Republican River and down the Republican to Fort Riley. [pg 332]

Mention is made of fish only twice in the entire log. We doubt that Muddy Creek or the East Laramie River is the type locality of *P. gulonellus*, because the flathead chub has not since been found in either of these streams. The most likely collection site for *P. gulonellus* is the North Platte River near the mouth of Sage Creek, in what is now Carbon County, Wyoming, where the expedition was camped for three days. This

species is known to occur in the North Platte River, and since the type locality is reported as "near Bridger's Pass" this is the probable location.

Range (Plate 21).--Upper mainstream and tributaries of Rio Grande, Pecos, Arkansas and North Platte Rivers; isolated populations in tributaries of the upper Missouri River.

Specimens examined.--Below are listed museum numbers, number of specimens (in parentheses), localities and year of collection. Series marked by asterisks (*) are intergrades tending toward *H. g. gulonella*. Literature reports are cited in the synonymy.

COLORADO: KU 4742 (162), Bent Co., Purgatoire R. at Las Animas, 1959; KU 4748 (105), Pueblo Co., Arkansas R. at west edge of Pueblo, 1959; KU 4758 (50), Fremont Co., Arkansas R. at Florence, 1959; KU 4769 (64), Fremont Co., Beaver Cr., 1959.

KANSAS: KU 2648 (2), Finney Co., Arkansas R., 1958; KU 2858 (13), Finney Co., Arkansas R. at Garden City, 1951; KU 3964 (12), Kearney Co., Arkansas R., 1958; * KU 4041 (2), Cheyenne Co., Republican R., 1958; KU 4732 (30), Hamilton Co., Arkansas R. at Kendall, 1959; * KU 4868 (1), Kansas-Nebraska line, Republican R. 1.5 mi. S. Hardy, 1959.

MONTANA: * MSC 1960 (8), Powder River Co., E. Fork of Powder R., 1957; MSC 2010 (64), Dawson Co., Redwater R., 1957.

NEBRASKA: * KU 2140 (2), Dawson Co., Platte R., at Gothenburg, 1931; * KU 4863 (20), Furnas Co., Republican R. at Cambridge, 1959; * UM (field no. 59-49) (74), Scotts Bluff Co., North Platte R. at Morrill, 1959; * UMMZ 133918 (17), Dixon Co., Logan Cr., 1939; * UMMZ 134813 (31), North Platte R., Neb.-Wyo. line, 1941; * UMMZ 135084 (14), Harlan Co., Beaver Cr. 0.25 mi. S Stamford, 1940; * UMMZ 135200 (41), Scotts Bluff Co., North Platte R. 1 mi. SE Henry, 1940; * UMMZ 135280 (59), Cherry Co., Niobrara R. 3 mi. SE Valentine, 1940; * UMMZ 135700 (25), Buffalo Co., South Loup R. 8 mi. N Miller, 1941; * UMMZ 135778 (54), Thurston Co., Logan Cr. 2.5 mi. W Pender, 1941; * UMMZ 135786 (25), Dixon Co., Logan Cr. 0.5 mi. NW Wakefield, 1941.

NEW MEXICO: KU 4219 (50), Colfax Co., Cimarron Cr. at Springer, 1958; KU 4235 (19), Mora Co., Sapello Cr. near Sapello, 1958; KU 4245 (157), Bernalillo Co., Rio Grande 12 mi. S Bernalillo, 1958; KU 4255 (22), Rio Arriba Co., Rio Grande at Velarde, 1958; KU 4266 (53), Sandoval Co., Rio Grande 2 mi. N Cochiti Pueblo, Marcelino Baca bridge, 1958; KU 4269 (91), San Miguel Co., Pecos R., 3 mi. S Pecos, 1958; KU 4274 (25), Sandoval Co., Jemez R. at Jemez Canyon Dam, 1958; KU 4294 (113), Guadalupe Co., Pecos R. 3 mi. N. Dilia, 1958; UMMZ 94897 (146), Pecos R. at San Tuan, 1926; UMMZ 94898 (1), Pecos R. at San Juan, 1926; UMMZ 118209 (68), Sapello Cr. at Sapello, 1937; UMMZ 133131 (7), Pecos R. 0.5 mi. N Santa Rosa, 1940; UMMZ 133136 (1), Rio Grande at Albuquerque, 1940. [pg 333]

OKLAHOMA: KU 2329 (1), Cleveland Co.-McClain Co. line, S. Canadian R., 1952; UOMZ 26355 (10), Cimarron Co., Cimarron R. 2 mi. N. Kenton, 1957; UOMZ 5917 (2), Cleveland Co., S. Canadian R. S Norman, 1925.

TEXAS: KU 3409 (18), Hemphill Co., Canadian R. at town of Canadian, 1955.

WYOMING: WU 2084 (4), Platte Co., N. Platte R. at Glendo, 1956; WU 2095 (3), Converse Co., N. Platte R. at Douglas, 1956; UMMZ 104064 (58), N. Platte R. below Guernsey Dam, 1937; * UMMZ 114642 (7), drainage ditch in Wind R. drainage, 1936; * UMMZ 114644 (20), drainage ditch at Riverton, 1936; * UMMZ 127518 (63), Weston Co., Beaver Cr., 1934; * UMMZ 127681 (20), Big Horn Co., Big Horn R. tributary, 1939; * UMMZ 136488 (9), Crook Co., Belle Fourche R. 15 mi. N Devil's Tower, 1941; * WU 2122 and two uncatalogued series at WU (13), Belle Fourche R., no precise locality or date; UMMZ 159969 (14), Natrona Co., N. Platte R. 2 mi. E Casper, 1950.

INTRASPECIFIC VARIATION

Two subspecies of *H. gracilis* are recognized by us: one northern and eastern, characteristically inhabiting large rivers (*H. g. gracilis*), and one southern and western, characteristically inhabiting small streams (*H. g. gulonella*). Other scientific names that have been applied to this fish in the past are listed in the synonymy.

H. g. gulonella is a chubby, deep-bodied fish, whereas *H. g. gracilis* is long and slender. The head of the creek subspecies is deeper and longer than that of *H. g. gracilis*, being rounded anteriorly when seen in sideview. The head of the large-river subspecies is acutely wedge-shaped in profile. *H. g. gracilis* has a larger orbit than *H. g. gulonella*. Fins of *H. g. gracilis* are more strongly falcate than those of the other subspecies. *H. g. gracilis* has a greater number of lateral line scales, pectoral rays and post-Weberian vertebrae than the creek subspecies. The large-river subspecies attains much larger size than does the creek subspecies (Plate 24). Except in areas of intergradation, complete separation of the two subspecies can be made on the basis of lateral line scales, pectoral rays, post-Weberian vertebrae and head-depth. The regressions of head-depth on standard length in *H. g. gracilis* from the Saskatchewan River (several localities) and in *H. g. gulonella* from Beaver Creek, Arkansas River Drainage (KU 4769) are shown in Plate 24.

Although values for the largest specimens of *H. g. gracilis* are omitted from Plate 24, the regression remains essentially linear to standard lengths of approximately 250 mm. On the basis of head-depth alone, separation of the two subspecies is possible in specimens larger than 40 mm. Similar results were obtained by using the regression of postorbital length on standard length, and could have been obtained by using other proportional measurements.

[pg 334]

NATURAL HISTORY

Habitat

The species inhabits alkaline streams with shifting sand bottoms where the waterlevel fluctuates considerably with heavy rains and melting snow. The flathead chub is found in silty water and often is the predominant species in streams that have high turbidity. The remarkable ability of this fish to withstand exceedingly high turbidity is illustrated by its predominance in the Little Missouri River, which has an average concentration of suspended silt two and one-half times that of the Missouri River at Kansas City (Personius and Eddy, 1955:42).

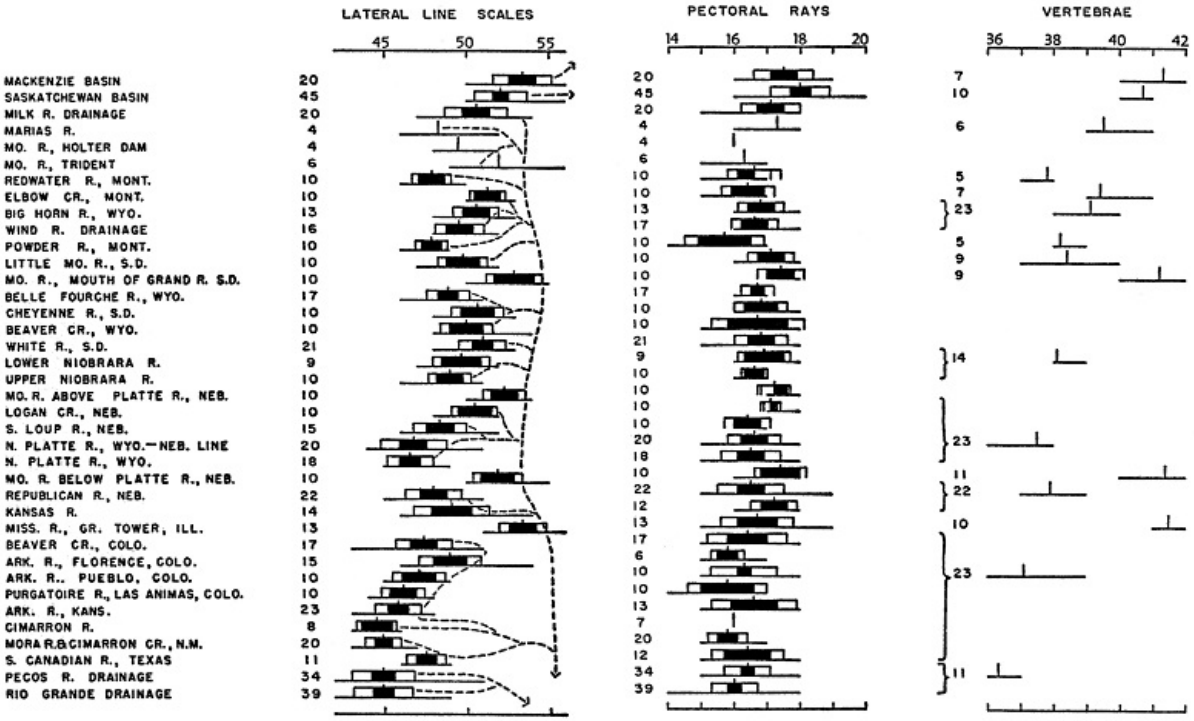


FIGURE 1. Graphic analysis of lateral line scales, pectoral rays and post-Weberian vertebrae in *Hybopsis gracilis*. In each symbol, horizontal line = range, vertical line = mean, open rectangle = one standard deviation on each side of mean, black rectangle = twice the standard error on each side of mean. Numbers to left of symbols = number of specimens examined from that locality; combined collections indicated by brackets. The dash-lines represent drainage patterns of rivers in which this species occurs.

H. g. gracilis is found in large rivers throughout its range, occasionally migrating into smaller streams, especially in the spawning season. It prefers the main channel of rivers in moderate to strong current. All series examined are from elevations lower than 3,000 feet. [pg 335]

H. g. gulonella occupies small rivers and creeks, preferring pools with moderate currents. In fall, dense concentrations of this subspecies have been found in small pools, where brush, driftwood or other debris deflects the current and prevents filling with drifting sand. Hundreds of flathead chubs were collected in such pools in the Purgatoire and Arkansas rivers. Specimens were also collected with ease in Beaver Creek, Colorado, from pools with murky water and slight flow, over bottoms of gravel and bedrock. No brush or other debris was near the pools. In each case the streams carried little water, although they undoubtedly carry greater volumes of water in spring and early summer after rains and spring thaws. The preferred bottom-type for this subspecies seems to be gently shifting sand. [pg 336]

H. g. gulonella is found in warm-water streams, whereas *H. g. gracilis* occurs in cooler water. The southwestern subspecies was taken in August in the Mora River drainage at Sapello (temperatures above 80° F.) but not at Mora (temperatures below 70° F.). In the Purgatoire River, a thriving population was found where the water temperature was 92° F., on September 6, 1959. In the Arkansas and Pecos rivers and the Rio Grande this subspecies is most abundant below the mountainous parts of the stream-courses, but at elevations higher than 4,000 feet on the plains.

Associated Species

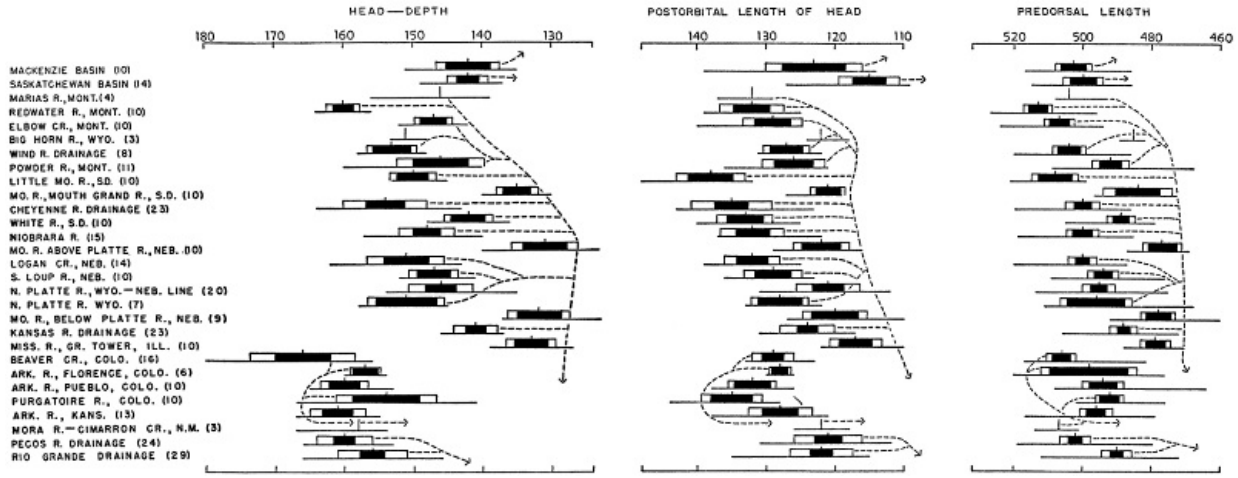


FIGURE 2. Graphic analysis of head-depth, postorbital length of head and predorsal length of *Hybopsis gracilis*, expressed as thousandths of standard length. Numbers in parenthesis = number of specimens examined from each locality. In each symbol, horizontal line = range, vertical line = mean, open rectangle = one standard deviation on each side of mean, black rectangle = twice the standard error on each side of mean. The dash-lines represent drainage patterns of rivers in which this species occurs. All measurements are of specimens 70 to 100 mm in standard length.

In the Pecos and Arkansas basins, species commonly taken with *H. g. gulonella* are *Catostomus commersonnii*, *Hybognathus placita*, *Notropis lutrensis lutrensis*, *Notropis stramineus missuriensis*, *Pimophales promelas*, and *Campostoma anomalum plumbeum*. The only spiny-rayed fishes that we have found with *H. g. gulonella* are *Lepomis cyanellus* and *L. humilis*, both of which are scarce. Associates of *H. g. gracilis* include the same species, plus other ostariophysan fishes such as species of *Carpiodes*, *Ictiobus*, and silt-adapted species of *Hybopsis* and *Notropis*. [pg 337]

We failed to find the flathead chub at any of 11 localities in the South Platte drainage, where we collected in September, 1959. Dr. George Baxter, of the Department of Zoology, University of Wyoming, told us that he has never found *H. gracilis* in that drainage. The fauna of the South Platte includes *Catostomus catostomus*, *Semotilus atromaculatus*, *Hybopsis biguttata*, *Hybognathus hankinsoni*, *Notropis cornutus frontalis*, *Etheostoma nigrum* and *E. exile*--species rarely if ever found with *H. gracilis*.

Ecologically, *H. g. gulonella* seems to be the counterpart of *Semotilus atromaculatus* in streams where the latter species is absent. Observations of *H. g. gulonella* in the Purgatoire River indicated that loosely-organized groups of flathead chubs congregated one to four inches above the bottom of pools, and near or under protective cover such as roots of vegetation or debris lodged against shore. Individuals moved about independently within the group (rather than as schools), and occasionally rose to the surface, perhaps for food. [pg 338]

Food

The flathead chub is chiefly carnivorous, but its food includes some aquatic vegetation (Table 1). Most organisms found in specimens (both subspecies) were terrestrial insects (Coleoptera, Diptera, Orthoptera); all insects were adult stages, except those designated as larvae in Table 1. Roundworms probably were parasites, rather than food.

Hubbs (1927:76) states that the food of young flathead chubs that were obtained from the Arkansas River System in New Mexico consisted "almost entirely of crustaceans (small ostracods and cladocerans to the exclusion of all else but an occasional larval or adult insect, etc.)."

Spawning Season

Specimens of *H. g. gulonella* that have been examined reach sexual maturity at approximately 65 mm standard length. Most specimens of *H. g. gracilis* less than 85 mm in standard length are immature, but larger specimens probably are mature.

The spawning season is in late summer, beginning in July and extending into September. Specimens from the Peace River, collected on August 10, 1952, include females that were mostly spent and tuberculate males. Males and females in spawning condition were collected in the Milk River in August of 1955. A large prespawning female was obtained in Red Deer River in June of 1952. A male from Fort McMurray had fairly well developed tubercles on August 9, 1955. A prespawning female was taken from the Saskatchewan River at Clarkboro Ferry on June 7, 1957. Tuberculate males were collected in the Powder River on June 30, 1957. Specimens from the White River in South Dakota, collected on July 7, 1934, include tuberculate males. The specimens discussed above are *H. g. gracilis* or intergrades tending toward that subspecies.

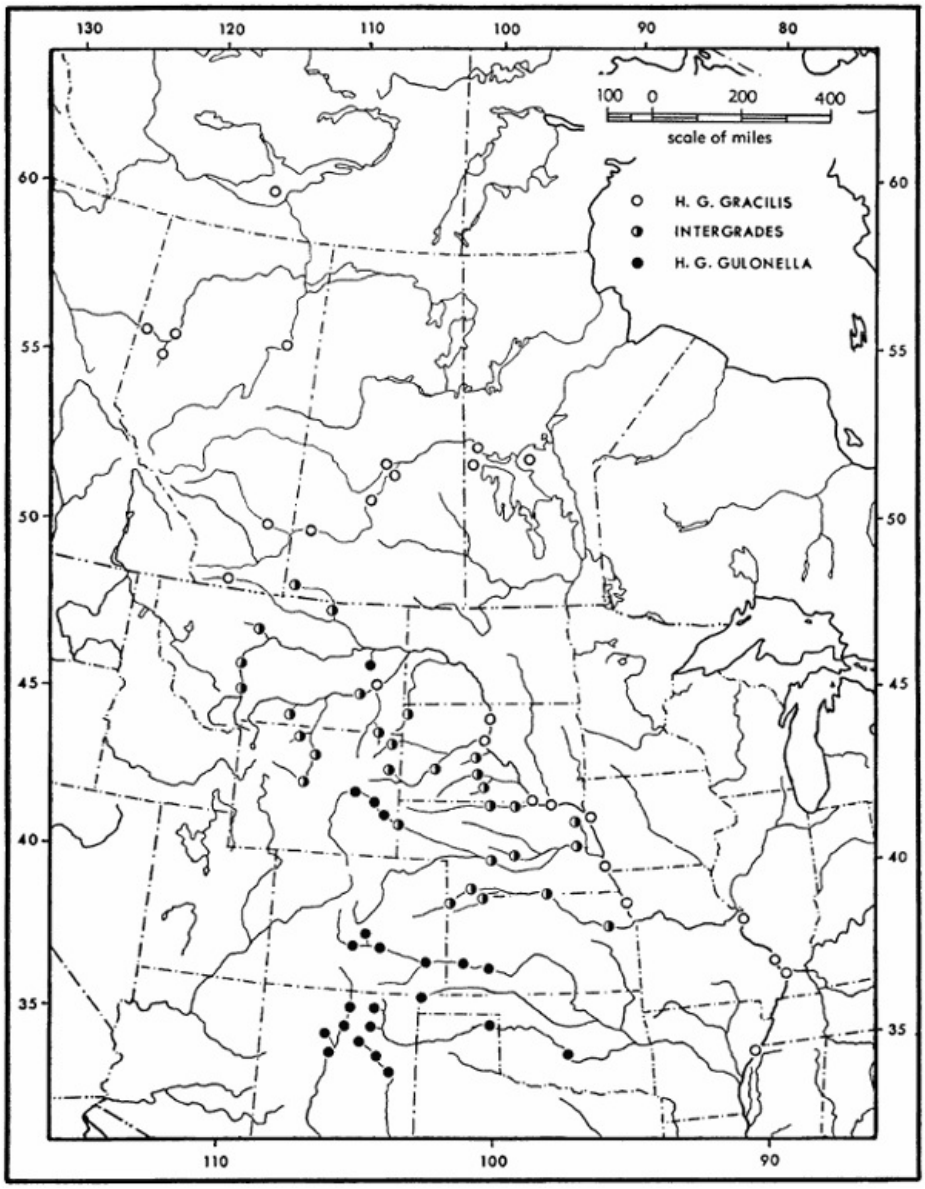
Specimens of *H. g. gulonella* collected in the Arkansas River at Pueblo and Florence, Colorado,

on September 7, 1959, include some tuberculate males, although most females are spent. On August 8, 1957, a series of flathead chubs that includes tuberculate males was collected in the Redwater River, Montana. In the Pecos River on August 25, 1958, spawning seemingly had been completed, although a few males still bore tubercles. [pg 340]

TABLE 1. ORGANISMS FOUND IN STOMACHS OF HYBOPSIS GRACILIS FROM VARIOUS LOCATIONS, EXPRESSED AS PERCENTAGE OF TOTAL VOLUME.

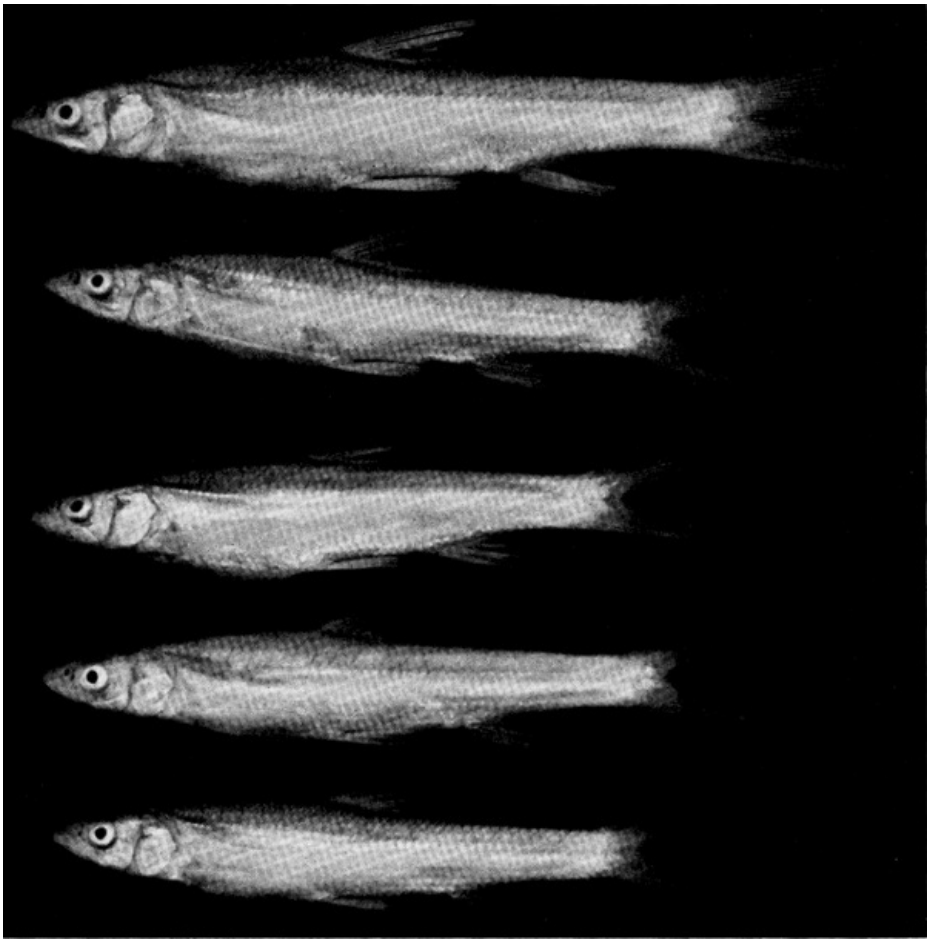
	S. Saskatchewan R., Clarkboro Ferry, Sask.	B: Milk R., Alberta	Missouri R., S. D.	Missouri R., Neb.	Arkansas R., Fremont Co., Colo.	Arkansas R., Pueblo Co., Colo.	Pecos R., San Miguel Co., N. M.
No. specimens examined	1	7	6	10	10	10	10
No. specimens containing food	1	6	1	2	1	3	7
KIND OF ORGANISM							
Aphasmidia	10.0	00.7	.....	03.0	.....	.....	.....
Arthropoda							
Araneae							
Argiopidae	.....	.....	.....	.....	04.0	.....	.....
Theridiidae	.....	.....	.....	.....	04.0	.....	.....
Insecta							
Ephemeroptera (nymph)							
Baetidae	.....	05.0	.....	.....	.....	.....	.....
Heptagenidae	.....	08.0	.....	.....	.....	.....	.....
Hemiptera							
Corixidae	35.0	00.3	.....	.....	.....	.....	.....
Hymenoptera							
Formicidae	.....	21.0	.....	.....	.....	.....	60.0
Coleoptera							
Staphylinidae	.....	01.7	07.0	.....	.....	.....	.....
Scolytidae	.....	13.3	70.0	.....	.....	.....	.....
Tenebrionidae	.....	05.7	.....	.....	70.0	.....	.....
Carabidae	.....	05.7	.....	.....	.....	01.0	.....
Curculionidae	.....	01.0	.....	.....	.....	.....	.....
Coccinellidae	.....	.....	.....	.....	.....	.....	09.0
Trichoptera (case)	.....	01.7	.....	.....	.....	.....	.....
Diptera							
Mymaridae	.....	00.3	.....	.....	.....	.....	.....
Empididae	.....	01.3	.....	.....	.....	.....	.....
Cecidomyiidae	.....	.....	.....	.....	04.0	.....	.....
Trachinidae	.....	00.7	.....	.....	.....	.....	.....
Simulidae	.....	06.7	20.0	.....	.....	.....	.....
Tabanidae	.....	.....	.....	.....	06.0	.....	.....
Chironomidae	.....	.....	.....	.....	06.0	.....	.....
Not identified to family	.....	01.0	.....	.....	.....	.....	.....
Orthoptera							
Locustidae	.....	07.7	.....	.....	.....	.....	.....
Tettigoniidae	.....	.....	03.0	70.0	.....	.....	09.0
Tetrigidae	.....	.....	.....	.....	06.0	.....	.....
Homoptera							
Fulgoridae	.....	05.0	.....	.....	.....	.....	01.0
Insect egg	.....	00.7	.....	.....	.....	.....	.....
Plants							
Cyanophyceae	.....	09.0	.....	.....	.....	99.0	20.0
Cyperaceae	.....	02.0	.....	.....	.....	.....	01.0
Zannichellia palustris	.....	00.3	.....	.....	.....	.....	.....
Vascular remains	55.0	.....	.....	27.0	.....	.....	.....
Miscellaneous							
Sand	.....	00.7		.....	.....	.....	.....
Pharyngeal tooth	.....	00.3	.....	.....	.....	.....	.....
Total (%)	100.0	99.8	100.0	100.0	100.0	100.0	100.0

Spawning apparently occurs when river levels recede to the seasonal lows. In late summer, temperatures of these rivers probably are maximal, their turbidities are reduced, and their sandy bottoms are stable. Underhill (1959) reports that this species is rare in the Vermillion River, a northeastern tributary of the Missouri River, except in autumn when large numbers occur near the mouth of the river. We suspect that this is associated with spawning.



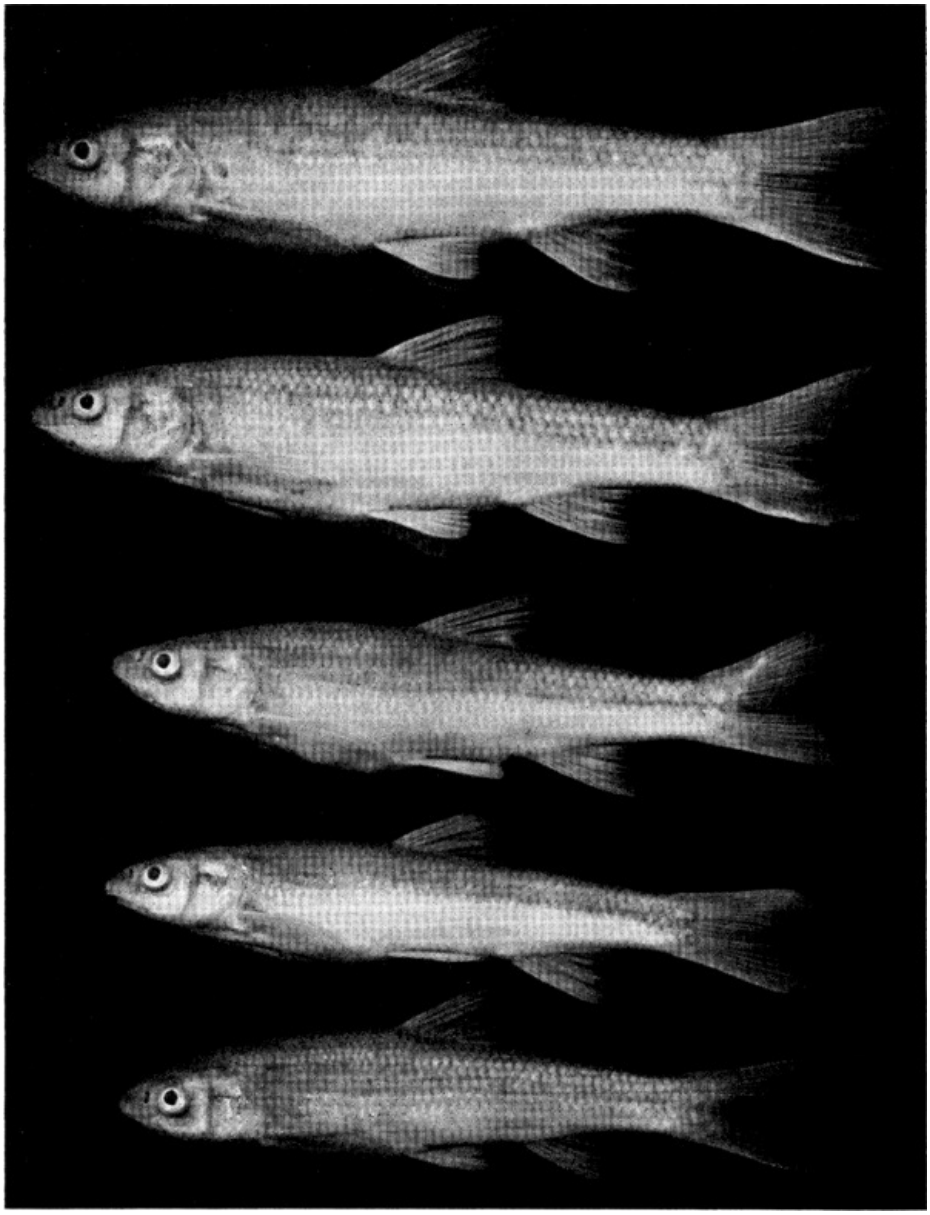
Distribution of collections examined.

PLATE 22



Hybopsis gracilis gracilis. Missouri River, Thurston County, northeast of Macy, Nebraska. Largest specimen 87.5 mm standard length.

PLATE 23



Hybopsis gracilis gulonella. Pecos River, San Miguel County, 3 miles south of town of Pecos, New Mexico. Largest specimen 91 mm standard length.

PLATE 24

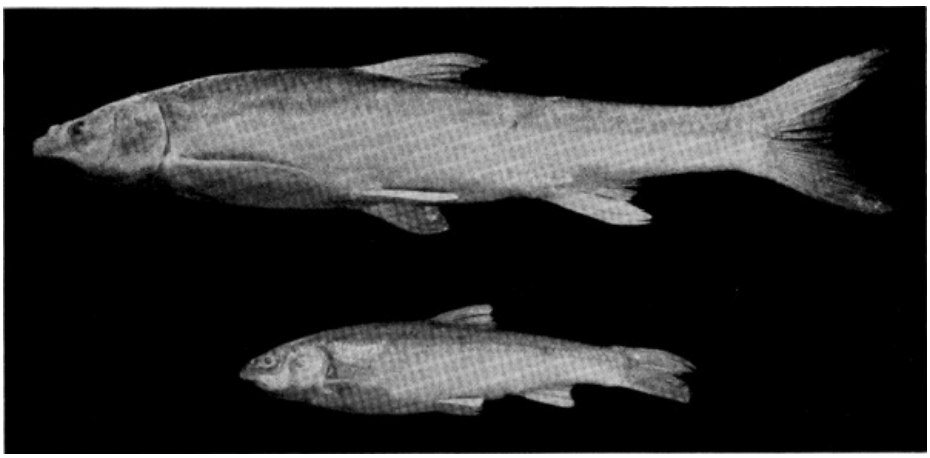


FIG. 1. Top: *Hybopsis gracilis gracilis*, 230.0 mm standard length, one of the largest specimens examined. Missouri River, Carson County-Walworth County line, 3 miles northeast of Mobridge, South Dakota, at mouth of Grand River.

Bottom: *Hybopsis gracilis gulonella*, 121.6 mm standard length, the largest specimen examined of this subspecies. Beaver Creek, Fremont County, 10 miles northeast of Florence, Colorado, on Highway 115.

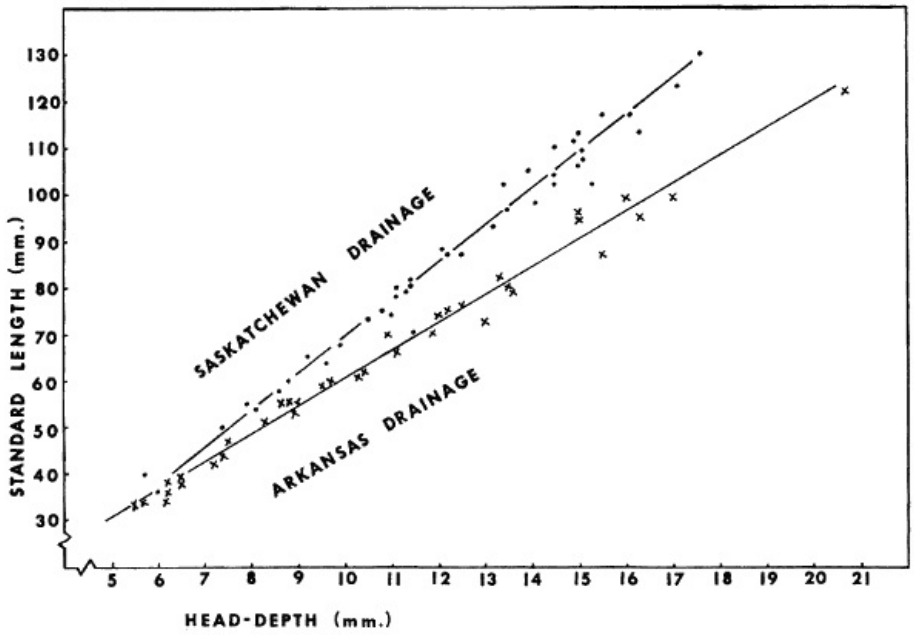


FIG. 2. Regression of head-depth on standard length in *Hybopsis gracilis gracilis* from the Saskatchewan River, and in *H. g. gulonella* from Beaver Creek, Arkansas River Drainage (KU 4769).

DISCUSSION

Hybopsis gracilis is highly variable in several morphological characteristics, including size and shape of head, body, and fins, and number of scales, vertebrae, and fin-rays. The variations are correlated in a way that indicates the existence of two subspecies. One of these, *H. g. gracilis*, attains large size, and has 1) a slender, streamlined body, 2) a depressed head that is acutely wedge-shaped in profile, 3) strongly falcate fins with the dorsal and pelvic fins originating anteriorly, and 4) many scales, vertebrae, and pectoral fin-rays. The second subspecies, for which *H. g. gulonella* is the oldest applicable name, is small, and has 1) a deep, chubby body, 2) head convex in dorsal contour (less depressed than in *H. g. gracilis*), 3) fins less falcate than in the latter subspecies, with the dorsal and pelvic fins originating more posteriorly, and 4) fewer [pg 341] scales, vertebrae, and pectoral fin-rays than *H. g. gracilis*. These differences are consistently expressed throughout the size-ranges of the subspecies, and in series collected at the same or nearby localities in several different years. Considerable variability was found in features other than those mentioned above, but individual variation among specimens from the same locality and adjacent localities is so great that none is diagnostic of subspecies. For example, orbital size and length of fins (but not their falcate shape) are variables that have little diagnostic value, although both features seem to vary in clinal fashion, with the higher values in the north.

Variation in *H. gracilis*, as shown in the graphic analysis (Figs. 1 and 2) and distribution map (Plate 21), presents two clines: a north-south cline and a large-river to small-river (mainly east-west) cline. The absence of *H. gracilis* from certain portions of river systems is a matter of concern. The species has not been found in the lower Arkansas River and the Rio Grande, nor in sandy tributary creeks in eastern Kansas and Missouri that appear to provide suitable habitat. It has already been noted that *H. g. gulonella* seems to be the ecological equivalent of *Semotilus atromaculatus* in streams in which *S. atromaculatus* is not found. *S. atromaculatus* occurs in creeks of eastern Kansas and Missouri, and may provide interspecific competition that prevents establishment of the flathead chub in these creeks. Regardless of cause, the gaps in distribution of *H. gracilis* tend to limit gene flow.

Many characters used in the separation of the two subspecies are known to be influenced by environmental conditions, especially temperature. Hubbs (1922, 1926, 1941), Schultz (1927), Vladykov (1934), Tåning (1952) and Weisel (1955), among others, have pointed out a correlation between temperature (or developmental rate of fish) and the number of vertebrae, scales, and fin-rays. Likewise, Martin (1949) and Hart (1952) have shown that the proportions of some body-parts vary in response to temperature during early development. In *H. gracilis*, the general nature of the clines found in a majority of characters (but not all characters) suggests a temperature influence. However, temperature-dependent variability that has so far been demonstrated experimentally in fishes is generally of lesser magnitude than the differences distinguishing *H. g. gracilis* and *H. g. gulonella*. To our knowledge, the most extreme differences that have been induced by modification of temperature are those reported for *Salmo trutta* by Tåning (1952:181-182), who states: "Shock treatment produced by especially great changes in temperature (*c.* 10-14° C), especially during the super-sensitive period [of somatic differentiation [pg 342] that fixes vertebral number] may produce ... a difference of 3-4 vertebrae ... in offspring of the same parents." The difference cited approximates that which distinguishes natural populations of *H. g. gracilis* and *H. g. gulonella*. Although we cannot assume that the sensitivity of the brown trout is the same as that of the flathead chub, the causative conditions in Tåning's study could scarcely be expected in nature; furthermore, it seems significant that extremely high (as well as

extremely low) mean numbers of scales and vertebrae were found at southern localities, and that low mean numbers of scales and vertebrae were found as far north as Wyoming and Montana. We think it likely that temperature does influence the expression of characters in *H. gracilis*, directly in individual development, and indirectly as a selective mechanism in the evolutionary process. The extent to which each kind of influence exists can be proved only by experimental work with both subspecies, which we hope to undertake at a later date.

Other environmental factors that may have selective influence in this species are rate of current, volume of flow, and turbidity. Interaction of these environmental factors could result in genetic fixation of morphological characters through natural selection. The characters that distinguish *H. g. gracilis* from *H. g. gulonella* seem adaptive to life in large rivers and small streams. Evidence that these characters are under limited, direct environmental influence is found among populations in the Arkansas River System. Although populations in the Arkansas River have no continuity with populations of *H. g. gracilis*, upstream-downstream variations like those found in other river systems are apparent, but in lesser degree. The direction of variation in the Arkansas River is the reverse of that in the Platte and other tributaries of the Missouri River. For example, the populations farthest upstream (Florence, Pueblo) have slightly higher mean numbers of lateral line scales than do populations from Kansas, downstream.

A remarkable effect of extreme parasitism in *H. gracilis* has been described by Hubbs (1927). Very young chubs that harbored numerous tapeworms (*Proteocephalus*) had unusually large numbers of lateral-line scales, large eyes, short snouts, small fins, small mouths lacking barbels, and coalescent nares (internarial bridge weak or absent). Some of these abnormalities presumably resulted from retention of larval characteristics of the fish, correlated with the degree of infestation by tapeworms. No teratological adults were found, indicating that severe infections prevent survival to maturity.

H. g. gracilis occurs in three separate river systems (Mackenzie, Saskatchewan, Missouri-Mississippi) from latitude 36° N to 66° N, and longitude 89° W to 123° W. *H. g. gulonella* exists as several seemingly-isolated populations in the upper parts of the Rio Grande, Pecos, South Canadian, Cimarron, Arkansas, Platte, and upper Missouri basins, from latitude 35° N to 48° N, and longitude 97° W to 100° W. [pg 343]

There is evidence of high mobility on the part of both subspecies, based on irregularity of their occurrence in certain localities. Many collections have been made in the Cimarron River in the vicinity of Kenton, Oklahoma, from 1925 to the present, but only one of these (in 1957) contained flathead chubs. Bait dealers who seine the South Canadian River in Dewey County, Oklahoma, have taken flathead chubs in abundance in some seasons, but not at all in others. Seasonal variation in abundance in the lower Vermillion River, South Dakota (Underhill, 1959:100) has been cited, and the number collected in the lower Kansas River near Lawrence has varied similarly. Many rivers occupied by *H. g. gulonella* (and by intergrades) are intermittent, and in some years their sand-filled channels become wholly dry for many miles. These factors probably promote mixing of the two subspecies, and may account, over long periods of time, for the wide dispersal of *H. g. gulonella* in the Missouri Basin. Flathead chubs are known from Pleistocene beds at Doby Springs, Oklahoma (the Doby Springs local fauna) (Smith, 1958:177). Drainage connections between the Arkansas, Kansas and Platte river systems existed in Kansan and Nebraskan times (Frye and Leonard, 1952:189-190). Populations that have subsequently become isolated in those rivers could be accounted for in this way. Flathead chubs could have entered the Rio Grande-Pecos system by stream-capture from the Arkansas System, in northeastern New Mexico or southern Colorado. *H. g. gracilis* undoubtedly entered the Saskatchewan and Mackenzie basins from the upper Missouri Basin, following glacial retreat (Walters, 1955:347).

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Transcriber's Note

The following changes have been made to the original text:

Table of Contents: page number of "Food" and "Spawning Season" changed from 339 to 338

Page 327: "abbreviated AU" changed to "abbreviated UA"

Page 344: "Societe Geologique" changed to "Société Géologique"

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