BRAIN PATTERNS IN FISHES OF THE GENUS <u>HYBOPSIS</u> IN RELATION TO FEEDING HABITS AND HABITAT

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PREFACE

Use of brain patterns as indicators of habitat and feeding habits in fishes has long been known. The present study was conducted to: (1) show correlation between brain patterns and habitat and feeding habits of well-known species of Hybopsis; (2) predict habitat and feeding habits of poorly-known species of Hybopsis; (3) illustrate variability within a species due to differences in habitat; (4) correlate number, size and location of taste buds with differences in facial and vagal lobes in Hybopsis.

This study has a companion study which deals with the structure of lateral-line canals and neuromasts in the genus Hybopsis.

Dr. Rudolph J. Miller directed the research and assisted in preparation of illustrations. Drs. L. Herbert Bruneau, Troy C. Dorris, Bryan P. Glass and Robert D. Morrison served on the advisory committee and critically evaluated the manuscript. Dr. George A. Moore also critically evaluated the manuscript. Dr. Robert D. Morrison and Bob Easterling assisted with the statistical analysis. Drs. Frank B. Cross, Carl D. Riggs, Royal D. Suttkus and John O. Whitaker donated or loaned specimens. Kenneth Beadles, Wayne Hadley, Darrell Hall and Harley Reno assisted in field collections. The assistance of these people is sincerely appreciated.

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CHAPTER I

INTRODUCTION

Behavior, in all except the most primitive animals, is largely dependent on a highly organized nervous system. In teleost fishes, organization of the neuraxis is less complex than in higher vertebrates, principally because of the relatively limited circuitry interposed between the several sensory systems and the central neuromotor apparatus. Although fishes lack the large association areas of higher vertebrates, Franz (1911) and Hemplemann (1926) suggested an associative function for the cerebellum; Sears (1934), Sanders (1940) and Botsch (1960) showed visually based associations in the tectum; and Hale (1956) demonstrated that the forebrain was involved in formation and performance of learned responses. Nonetheless, as Papez (1929) demonstrated, the teleost brain is developed primarily on the reflex level, with each reflex dealing with some important reaction to its environment. This type of brain reflects, more clearly then that of higher vertebrates, the correlation between sensory adaptations and principal modes of activity. Characteristic of some fish species is hypertrophy of particular brain lobes, especially the gustatory components of the medulla. An elaborate system of taste buds has developed in the mouth and palatal organ of the carpsucker, Carpiodes velifer, resulting in remarkable expansion of the vagal lobes (Miller and Evans, 1965). In some Gadidae, Cyprinidae and Catostomidae, where external taste buds are especially dense, the facial lobe is substantially enlarged (Evans, 1935; Evans, 1952; Miller and Evans, 1965). Since the development of sensory lobes often reflects hypertrophy of peripheral sensory mechanisms, inferences about the functional significance of these sensory modalities may be made with reasonable confidence. However, the technique of functional analysis based on morphological features should be used, when possible, in concert with behavioral observation and experimentation. Correlations between development of peripheral sensory systems and brain lobes will be discussed more thoroughly in the following sections.

Various taxonomists have attempted to use brain morphology as a taxonomic character to identify phylogenetic affinities, usually with scant success. Lissner (1923) attempted to construct a classification using brain patterns but finally concluded that ecological factors had such a profound influence that brain lobes could not be used in classification. Svetovidov (1953) supported the idea that brain patterns, particularly the position of the nasal capsule in relation to the olfactory lobes, could be used as diagnostic characters in a number of systematic groups. He also believed that in comparative studies among species from distantly related groups, ecological influences on the brain lobes were overshadowed by "...differences caused by peculiarities of the brain." Miller and Evans (1965) pointed out that major differences in sucker brains among subfamilies reflect an early division of these groups, but concluded that the principal benefit of brain pattern studies lies in the understanding of sensory specializations at the species level. Most investigators have concluded that brain pattern studies are most useful in providing insight into behavioral and ecological adaptations of fishes, although comparative studies may shed some light on phylogenetic relationships among the higher taxa.

Prior to the present time, there have been no detailed systematic evaluations using brain patterns within a single, speciose, highly variable genus. The polytypic genus Hybopsis, as now recognized, consists of 21 nominal species which probably constitute an unnatural grouping. Morphology and habitat preferences are extremely varied within the genus. While study of the sensory mechanisms may contribute to an understanding of taxonomic relationships among species, the aim of the present analysis is to provide a better understanding of the ecology of the species of Hybopsis. Except for members of the subgenus Nocomis, the ecology of the group is poorly known. Behavioral studies of well-known species correlated with brain patterns and peripheral sensory development can be used to make reasonable inferences about ecological requirements of little-known species.

CHAPTER II

MATERIALS AND METHODS

Specimens were obtained through gifts and loans from institutional museums and by personal field collections. Fixation was in 10 per cent formalin or Bouin's fluid followed by appropriate washing, water for formalin and alcohol for Bouin's, and storage in 50 per cent isopropanol.

Counts and Measurements

Morphometric data were taken according to Hubbs and Lagler (1947). Standard length (SL), head length (HL) and head width (HW) were measured to the nearest 0.1 mm and eye length (EL) to the nearest 0.01 mm.

Brains were inspected by making incisions with a single-edge razor blade in the cranium across the nasal region between the posterior nares, from the top of the orbits posteriad past the supratemporal canal and thence across the nape. The incised area was picked off with forceps. Forceps with ultrafine tips were used to remove the remaining soft tissue from the exposed brain. Close adherence of the pia mater to the brain surface necessitated extreme care to prevent damage to the brain during its removal. Presence of the pia mater was indicated by the occurrence of chromatophores on the brain surface. Each brain was examined with a dissecting microscope equipped with a Whipple disc. Grids on the disc were calibrated for each magnification with a stage micrometer. Sixteen measurements were taken to the nearest 0.01 mm from each brain (Fig. 1). An outline drawing of the brain of a selected specimen from each species was prepared on graph paper with the aid of a Whipple disc. Drawings were originally scaled at 30 to 1 and later reduced or enlarged to the same total size in order to evaluate differences previously noted in the brain lobes.

Barbels from selected specimens of each species were removed, dehydrated, cleared and embedded in paraffin (Guyer, 1953). Sections were cut with a rotary microtome at 10 microns, stained in Harris' hematoxylin and counterstained in eosin. Sections were examined using a binocular compound microscope for determination of histological differences and similarities among species. Numbers, lengths and proximal diameters of taste buds were recorded from sections randomly selected from distal, intermediate and proximal portions of the barbels.

Serial sections of the body surface and mucus lining of the buccopharyngeal cavity were examined for the presence of taste buds. Heads of specimens selected for serial sections were severed posteriad to the supratemporal canal, decalcified with four per cent hydrochloric acid in 80 per cent isopropanol for two weeks and dehydrated in acetone. Heads of larger specimens were split longitudinally to enhance decalcification, dehydration and infiltration. Paraffin infiltration was performed in a vacuum oven by reducing the pressure approximately 250 mm of Hg below atmospheric pressure. Five regions were selected for numerical determination of external and internal taste bud density because of the ease and precision with which the regions could be located: tip of snout (region 1) = immediately anterior to, but not through, the

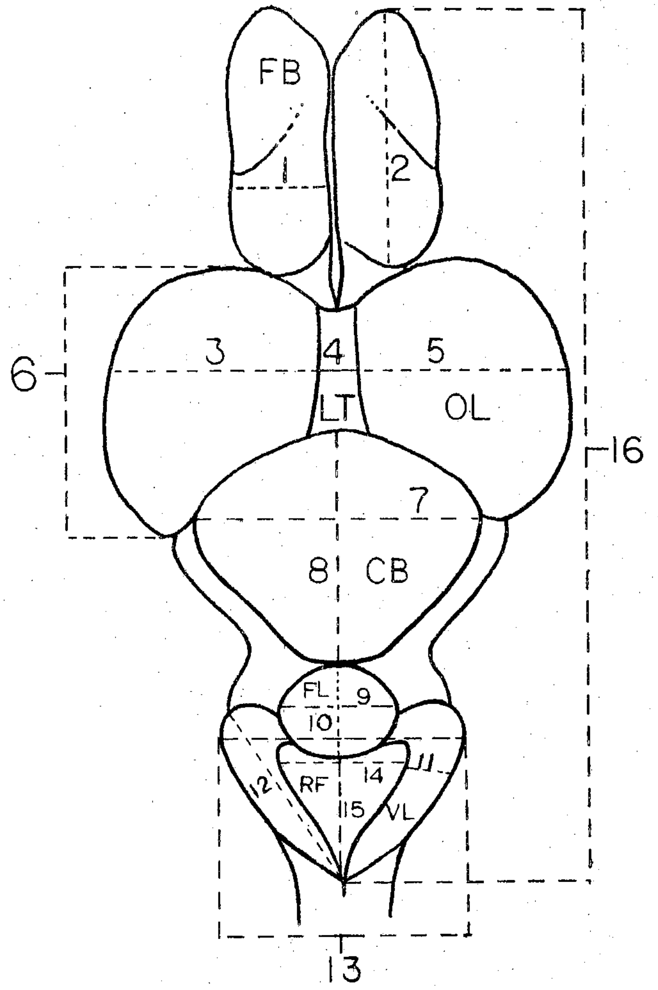

Fig. 1. Brain Pattern in *Hybopsis storeriana* Illustrating Brain Lobe Position and Method of Measurement.

FB = forebrain lobe
1 = forebrain width
2 = forebrain length
OL = optic lobe
3 = optic width
3-5 = total optic width
6 = optic length
LT = longitudinal tori
4 = tori width
CB = corpus cerebellum
7 = cerebellum width
8 = cerebellum length

FL = facial lobe
9 = facial width
10 = facial length
VL = vagal lobe
11 = vagal width
12 = vagal length
13 = total v. width
RF = rhomboid fossa
14 = r. fossa width
15 = r. fossa length
16 = total brain length

nasal rosette; anterior of nasal rosette (region 2) = that part of the snout containing the most anterior olfactory lamellae and lips; posterior of nasal rosette (region 3) = that part of the snout immediately behind the posterior edge of the olfactory rosette; posterior of retina (region 4) = that region immediately behind the posterior part of the retina; anterior of corpus cerebellum (region 5) = immediately posterior to the most anterior edge of the corpus (includes the pharyngeal cavity). Taste buds in every fourth section were counted until 10 sections had been counted.

Statistical Analysis

An IBM computer was used to make a statistical analysis of all quantitative variables. Total brain length was assumed as the independent variable with all other brain measurements employed as dependent variables. Variances and standard deviations adjusted for the independent variable were computed for all dependent variables. Due to the similarity of variance in most lobes only the optic lobe was used for illustrative purposes (Fig. 9). Tests for determination of lobe differences among species were made. Linear regressions were determined for each dependent variable. The null hypothesis of homogeneity of regression was proposed and tested with the appropriate "F" value. If the slopes were judged homogeneous, the adjusted means were tested by the appropriate "F" value. Means that were judged not to be homogeneous were tested among species to determine species differences. "T" values were determined by use of the inverted Doolittle method (Graybill, 1961). Significance for all tests is at the one per cent confidence level. Nine of the 15 dependent variables were judged to have homogeneous regression slopes and non-homogeneous adjusted means.

Materials Examined

Species names follow Moore (1957) except for *Hybopsis* (*Nocomis*) sp. During the course of the present study 394 specimens involving 21 species of the genus *Hybopsis* were examined. *H. monacha* was not available for study and *H. cahni* was limited to a single specimen. All other species were represented by two or more specimens. Specimens examined are listed below with the number of specimens from each collection in parentheses. Numbers separated by hyphens indicate the range of standard length in millimeters. Abbreviations for institutional museums include: Oklahoma State University (OAM), Kansas University (KU), Tulane University (TU), University of Texas (UT) and University of Richmond (UR).

Hybopsis aestivalis (Girard), speckled chub: (8), 17:X:1964, Arkansas R., Kay Co., Okla., 30.4-43.9; (4), 23:VII:1964, Red R., Bryan Co., Okla., 42.1-47.1; (15), 15:XII:1963, Arkansas R., Sequoyah Co., Okla., 37.8-48.2; (16), 21:VII:1963, Elm Fork of Red R., Greer Co., Okla., 38.4-48.2; (7), 8:III:1961, UT 293, San Marcos R., Gonzales Co., Tex., 35.1-51.6; (5), 1:IV:1961, KU 5976, Blanco R., Caldwell Co., Tex., 45.6-48.5; (12), 8:IV:1965, Cimarron R., Payne Co., Okla., 27.9-41.4; (1), 31:VIII:1964, Powell R., Claiborne Co., Tenn., 51.6; (4), 6:XII:1960, KU 7266, Wabash R., Clark Co., Ill., 45.9-47.8; (5), 22:VII:1964, North Fork of Ninnescah R., Sedgewick Co., Kan., 49.5-53.9; (2), 22:VI:1949, OAM 3337, Wolf Cr., Harmon Co., Okla., 46.4-54.0; (7), 17:X:1963, Red R., Bryan Co., Okla., 30.2-39.2; (3), 16:VIII:1947, OAM 1870, Salt Fork R., Alfalfa Co., Okla., 46.5-50.6; (7), 18:II:1950, OAM 4068, Red Rock Cr., Pawnee Co., Okla., 26.7-39.1; (2), 17:IV:1963, Rio Grande, Coahuila, Mex., 33.6-36.5; (4), 14:IV:1963, KU 8319, Pecos R., Chaves Co., N. Mex., 32.7-33.0; (3), 23:IV:1964, Pecos R., Chaves Co., N. Mex., 34.2-36.5; (5), 25:VII:1955, OAM 5269, Red R., Bryan Co., Okla., 41.2-48.0; (2), 1:V:1954, OAM 5195, Red R., Bryan Co., Okla., 37.1-40.2; (1), 21:VII:1952, Jimenez, Coahuila, Mex., 46.1; (5), 16:II:1952, Pearl R., Marion Co., Miss., 36.3-41.1; (2), 26:XI:1951, OAM 5350, Guadalupe R., Kendall Co., Tex., 37.0-40.2; (4), 17:VIII:1965, North Fork of Red R., Tillman Co., Okla., 31.7-45.3; (9), 17:VIII:1965, North Fork of Red R., Kiowa Co., Okla., 39.3-48.3; (5), 19:IV:1964, Clear Fork of Brazos R., Young Co., Tex., 34.4-41.4.

Hybopsis amblops (Rafinesque), bigeye chub: (8), 31:VIII:1964, Powell R., Claiborne Co., Tenn., 36.9-59.4; (1), 4:V:1963, Sallisaw Cr., Sequoyah Co., Okla., 62.2; (6), 8:IV:1963, KU 7677, Current R., Shannon Co., Mo., 29.7-54.0; (6), 29:XII:1962, TU 28818, Strong R., Simpson Co., Miss., 42.0-52.2; (5), 19:IX:1963, Sugar Cr., Park Co., Ind., 32.3-54.8.

Hybopsis bellica (Girard), southern chub; (4), 7:VIII:1962, TU 29449, Toxaway R., Transylvania Co., N. C., 33.6-85.1; (4), 29:VIII:1964, Warren-Hancock Co., Ga., 43.0-55.0.

Hybopsis biguttata (Kirtland), hornyhead chub: (2), 5:IV:1953, OAM 5788, Sycamore Cr., Ottawa Co., Okla., 34.5-43.9; (11), 5:IX:1937, Saline R., Mich., 49.9-85.6; (3), 9:IX:1964, Kings R., Carroll Co., Ark., 57.0-70.0; (3), 10:X:1965, Barron Fork Cr., Cherokee Co., Okla., 45.0-59.0.

Hybopsis cahni Hubbs and Crowe, slender chub: (1), 31:VIII:1964, Powell R., Claiborne Co., Tenn., 46.0.

Hybopsis crameri Snyder, Oregon chub: (3), 10:VI:1963, Willamette R., Lane Co., Ore., 25.0.

Hybopsis dissimilis (Kirtland), streamline chub: (2), 4:IV:1964, KU 8000, Buffalo R., Marion Co., Ark., 62.8-68.1; (8), 31:VIII:1964, Powell R., Claiborne Co., Tenn., 56.9-80.6; (3), 9:IX:1949, St. Francis R., Mo., 73.2-79.3.

Hybopsis gelida (Girard), sturgeon chub: (1), 17:VII:1940, Mississippi R., Jackson Co., Ill., 52.2; (4), Kaw R., Douglas Co., Kan., 43.4-46.0.

Hybopsis gracilis (Richardson), flathead chub: (5), 28:VIII:1958, KU 4235, Mora R., Mora Co., N. Mex., 29.7-75.4; (6), 4:VI:1963, KU 8353, Greenhorn Cr., Pueblo Co., Colo., 35.3-94.4; (3), 26:VIII:1959, OAM 5421, Rio Grande, Bernalillo Co., N. Mex., 45.0-47.6; (4), Redwater Cr., McCone Co., Mont., 63.0-64.5.

Hybopsis harperi (Fowler), redeye chub: (7), 30:V:1951, Russ Cr., Jackson Co., Fla., 36.7-42.3; (13), 11:IV:1955, Ichtuchnee Spring, Columbia Co., Fla., 37.7-50.8.

Hybopsis hypsinota (Cope), highback chub: (2), OAM 5590, Alabama R., Ala., 45.0-48.7; (5), 15:II:1964, Colds Springs, Meriwether Co., Ga., 39.7-48.7.

Hybopsis insignis Hubbs and Crowe, blotched chub: (12), 31:VIII:1964, Powell R., Claiborne Co., Tenn., 45.5-52.3; (2), 20:V:1959, South Indian Cr., Tenn., 65.3-73.5

Hybopsis labrosa (Cope), thicklip chub: (2), 7:IX:1964, North Fork of Saluda R., Pickens Co., S. C. 46.5-48.0

Hybopsis leptocephala (Girard), Carolina chub: (7), 6:IX:1964, Iredell Co., N. C. 37.8-58.6; (1), 4:VII:1958, OAM 5992, Roanoke R., Montgomery Co., Va., 48.0; (4), 7:IX:1963, UR 1973, Catawba R., Burke Co., N. C. 48.0-60.0.

Hybopsis micropogon (Cope), river chub: (10), 31:VIII:1964, Powell R., Claiborne Co., Tenn., 38.7-50.1; (5), 21:V:1959, Catatonk Cr., Tioga Co., N. Y. 42.0-106.9; (3), 2:VII:1963, UR 1755, North Fork of Holston R., Smyth Co., Va., 77.5-98.1.

Hybopsis meeki Jordan and Evermann, sicklefin chub: (8), 1:VIII:1941, OAM 285, Mississippi R., Jackson Co., Ill., 21.0-47.9; (1), Missouri R., Jackson Co., Mo., 45.0.

Hybopsis (*Nocomis*) sp., bull chub: (18), 5:VII:1961, OAM 5991, Blackwater R., Franklin Co., Va., 56.7-98.0.

Hybopsis plumbea (Agassiz), northern chub: (1), 15:V:1964, Bluewater Cr., Carbon Co., Mont., 54.0; (4), 22:VI:1961, KU 6872, Bighorn R., Bighorn Co., Wyom., 33.5-43.4; (9), 28:VIII:1965, Cliff Lake, Madison Co., Mont., 45.7-93.1.

Hybopsis rubrifrons (Jordan), redface chub: (1), 16:V:1948, Broad R., Oglethorpe Co., Va., 54.7; (6), 23:VII:1962, TU 29593, Toxaway R., Pickens-Oconee Co., S. C. 51.5-58.7; (2), 29:VII:1964, Ogeechee R., Warren-Hancock Co., Ga., 47.0-51.0.

Hybopsis storeriana (Kirtland), silver chub: (3), 15:XII:1963, Arkansas R., Pope Co., Ark., 58.5-72.4; (5), 8:XII:1964, Wabash R., Vigo Co., Ind., 45.8-88.3; (7), 26:VII:1964, Red R., Bryan Co., Okla., 44.0-85.7; (2), 19:IX:1963, OAM 5632, Mississippi R., Scott Co., Iowa, 57.0-64.0.

Hybopsis x-punctata Hubbs and Crowe, gravel chub: (6), 24:VII:1946, OAM 2389, Illinois R., Sequoyah Co., Okla., 43.0-59.3; (2), 25:VIII:1946, OAM 2384, Illinois R., Sequoyah Co., Okla., 53.6-57.0; (1), 9:IX:1964, Black R., Lawrence Co., Ark., 49.4.

CHAPTER III

HABITAT AND DISTRIBUTION

The present genus *Hybopsis*, as recognized by Bailey (1952), includes the former genera *Couesius*, *Erimystax*, *Hybopsis*, *Macrhybopsis*, *Nocomis*, *Oregonichthys*, *Platygobio* and *Yuriria*. *Hybopsis* (*Yuriria*) *alta* is a Mexican species and is not included in the present study. The genus as described by Moore (1957) is

> Barbels (*H. hypsinota*, *H. harperi* in the south and *H. amblops* often lack them) usually at the terminus of the maxilla. In *H. plumbea* the barbel is not terminal but placed on the anterior surface of the maxilla anteriad to its posterior end. Eye variable in size, small to large. Mouth usually horizontal, rather small, and with lower jaw included, but in some species rather large, oblique and nearly terminal. Body usually slender and little compressed. Teeth vary from 4-4 to 2,4-4,2 usually with poorly developed grinding surfaces. Color pattern variable, some species very silvery and without a lateral band, others with a lateral band or conspicuous spots on back and sides; fins bright colored in breeding individuals of some species. Intestine is usually short but looped across the stomach in *H. leptocephala* and *H. bellica*. Size small (50 mm) to large (300 mm).

According to Hubbs and Crowe (1956) and others, the genus *Hybopsis*, as it now stands, is an "unsteady assemblage" of cyprinid fishes of extreme diversity, not only in morphology but in habitat preference. Habitats vary from low-gradient, silty streams of the Great Plains to swift, clear, gravelly streams of northern and eastern North America.

Hybopsis aestivalis is found in the mainstream of rivers and larger tributaries of the Mississippi and Rio Grande systems and in the Gulf Coast rivers of Texas (Moore, 1957). It is divided into six nominal subspecies (Hubbs and Ortenburger, 1929): H. a. aestivalis (Girard), H. a. australis (Hubbs and Ortenburger), H. a. tetranemus (Gilbert), H. a. hyostomus (Gilbert), H. a. sterletus (Cope) and H. a. marconis (Gilbert). According to Forbes and Richardson (1908), H. aestivalis is found over sand, but adults collected in Oklahoma were nearly always taken over areas of fine to coarse gravel interspersed with sand. Juveniles were taken over sand and silt bottoms.

Hybopsis amblops is scattered throughout the central and southeastern states from Lake Ontario, west to southern Michigan, south to eastern Oklahoma, Arkansas, Louisiana, Mississippi, Alabama and Georgia (Moore, 1957; Forbes and Richardson, 1908). It is most often collected in small or moderate-size streams of moderate gradient. Habitat preference is usually sand and fine gravel in pools and riffles (Trautman, 1957). Evidently this species is extremely intolerant of silt and other pollutants, as evidenced by a rapid decline in numbers with increased turbidity and pollutants in Ohio and Illinois streams (Trautman, 1957; Larimore and Smith, 1963).

Hybopsis bellica is restricted to the southeastern states from the Savannah River in Georgia westward through Alabama (Moore, 1957) and into the Gulf Coast drainage in Louisiana (Eddy, 1957). No published material on habitat preference was found.

Hybopsis biguttata is one of the most widely distributed chubs, ranging from New York westward to Wyoming and Colorado and south to eastern Oklahoma, northern Louisiana and Tennessee (Moore, 1957). This species normally inhabits small to moderate-sized, clear streams with gravel bottoms. Trautman (1957) suggests that its extreme range may be because it is more tolerant of changes in turbidity, stream size and current than other species of the subgenus Nocomis. However, H. biguttata has become less common or absent in some areas because of increased siltation and intermittency of flow (Deacon and Metcalf, 1961).

Hybopsis cahni evidently has a very restricted range in the Clinch and Powell rivers of eastern Tennessee. All known specimens (15) were collected in that area (Hubbs and Crowe, 1956; Davis and Reno, 1966). No publication relative to its habitat has been found, but two specimens collected in the Powell River in 1964 were taken from an area of clear swift water less than 18 inches deep. Bottom materials included cobbles and coarse gravel.

Hybopsis crameri is the only west coast representative of the genus. This species is apparently restricted to the Willamette and Umpqua rivers of Oregon (Eddy, 1957; Moore, 1957). Data on the preferred habitat of this species have not been located.

Hybopsis dissimilis is found throughout the Tennessee and Ohio River systems from Indiana to New York, southward to Tennessee and North Carolina, with a subspecies in the Ozark Uplift of southern Missouri and northern Arkansas (Moore, 1957). Distribution records prior to 1956 must be viewed with caution because of the inclusion in this nominal species of the presently recognized H. x-punctata. H. dissimilis is found on riffles and bars of large creeks and small rivers where the current is sufficient to keep coarse sand and gravels silt-free (Trautman, 1957). Trautman also indicated H. dissimilis is intolerant of silt and other pollutants, since a rapid decline in numbers occurs with increased siltation and pollution.

Hybopsis gelida is found in the Mississippi River basin from southern Illinois northward to Montana and Wyoming (Moore, 1957). Bailey and Allum (1962) mapped the range in the Mississippi River as far south as Cairo, Illinois, and westward in the Missouri River drainage, but *H. gelida* ascends neither the Ohio River nor the Mississippi River above its confluence with the Missouri River. Material available to me indicates that the southern limit in the Mississippi River is at least Grand Tower, Illinois. *H. gelida* is normally found in the main channels of larger rivers, usually over gravel, and it can tolerate the heavily silted streams of the Missouri River system (Bailey and Allum, 1962). The apparent spotty distribution of this species may be attributed to predominance of sandy stream bottoms in much of its range.

Hybopsis gracilis, according to Olund and Cross (1962), is found in the Mackenzie and Saskatchewan River systems and eastward to Lake Winnipeg in Canada. In the United States it is found in the Missouri River system continuously from the western high plains, in the Mississippi River as far south as Barfield, Arkansas, and upstream above its confluence with the Missouri River and into the Ohio River above its mouth. It is also found in the headwaters and tributaries of the Arkansas River system in eastern Colorado, western Kansas and the Oklahoma Panhandle and in restricted areas of the upper Rio Grande and Pecos River in New Mexico. Three specimens taken from the Snake River indicate a transfer, probably by fishermen, across the continental divide from the Wind River (Simon, 1964). *H. gracilis* is found in sandy-bottomed, alkaline streams which are subject to extreme changes in water level. Normally it is found in main channels of large rivers with moderate to strong currents. *H. gracilis* exhibits an extreme tolerance to silty conditions and is often the predominant species in streams with high turbidity (Olund and Cross, 1962).

Hybopsis insignis is found in the Cumberland River of Kentucky, Duck River system of Tennessee and the Tennessee River system of Tennessee, Georgia, North Carolina, Virginia and northern Alabama (Hubbs and Crowe, 1956; Moore, 1957). It is normally found in clear-water riffles over coarse gravel in moderate to large sized rivers.

Hybopsis harperi is restricted to northern Florida and adjacent parts of Alabama (Hubbs and Crowe, 1956). Its habitat includes springs, small spring-fed creeks with sand or mud bottoms, limestone sinks and caves (Bailey, Elliott and Lavett, 1954; Marshall, 1947).

Hybopsis hypsinota is restricted to the Santee River basin of North and South Carolina (Moore, 1957). No published data were found on its preferred habitat.

Hybopsis labrosa is confined to the Santee River system of North and South Carolina (Moore, 1957). No data were found on its habitat.

Hybopsis leptocephala is found on the Atlantic Coast from the York River of Virginia to the Savannah River of South Carolina and in the Gulf Coast drainage in the upper New River system of Virginia (Burton and Odum, 1945). Smith (1907) indicated that H. leptocephala preferred larger streams and avoided smaller ones, but Lachner (1952) collected specimens from small streams of the Piedmont region. Generally this species inhabits clear waters of moderate to fast flow over clean gravel bottoms (Raney, 1947).

Hybopsis meeki ranges throughout the Mississippi, Missouri and lower parts of the Kansas rivers. Upstream limit in the Missouri River is at the mouth of the Little Missouri River. It occurs downstream in the Mississippi River to southeastern Missouri (Bailey and Allum, 1962). Preferred habitat is in the strong currents of large silty rivers over fine sand or silt bottoms.

Hybopsis micropogon is found in the Wabash River system and lower peninsula of Michigan to the Lake Ontario basin, southward on the Atlantic Coast from the Susquehanna River system of New York to the James River system of West Virginia and on the uplands of the western Appalachian slope to the Tennessee River tributaries in Georgia and Alabama (Burton and Odum, 1945; Hubbs and Lagler, 1947). It should be noted that distribution records of *H. micropogon* prior to 1966 must be viewed with care since the description of a new species of the subgenus *Nocomis* is under study by E. A. Lachner and R. E. Jenkins. *H. micropogon* is usually found over sand and gravel or rubble in large, clean, clear rivers of the region.

Hybopsis monacha is found in the Tennessee River system of Tennessee, Virginia, North Carolina, Georgia and Alabama (Moore, 1957). No specimens were available for study.

Hybopsis (*Nocomis*) sp. is a new species to be described by E. A. Lachner and R. E. Jenkins. This species is found in the James, Chowan, Roanoke, Tar, Neuse and upper New rivers of the central Appalachian region.

Hybopsis plumbea is widespread throughout most of the Great Lakes region and in the Mackenzie, Hudson, Delaware, upper Missouri and Frasier River systems and in many lakes in the Northwestern United States and Canada (Eddy, 1957). *H. plumbea* inhabits cold lakes and streams, apparently preferring smaller streams. In some areas the species has become well established in irrigation canals (Simon, 1946).

Hybopsis rubrifrons is confined to the Altamaha River system of Georgia and adjacent parts of South Carolina (Moore, 1957). No publication pertaining to preferred habitat was found.

Hybopsis storeriana is widely distributed from Ontario to the Red River of Wyoming, southward to the Red River of Oklahoma and Texas and eastward to the Alabama River system (Moore, 1957). The silver chub is found in lakes and larger streams, preferring deeper waters which have sand and/or fine gravel bottoms. Normally a pool species, it will inhabit riffles if siltation is heavy (Trautman, 1957). H. storeriana inhabits large silty rivers of the Great Plains region, but it appears to seek refuge in smaller tributaries during times of flooding when the larger streams are carrying a heavy silt load.

Hybopsis x-punctata is found in the Ohio River basin from Illinois to Pennsylvania and Kentucky, the Thomas River of Ontario, and the Mississippi River system from Wisconsin and Minnesota to the Ozark uplands of Kansas, Missouri, Oklahoma and Arkansas (Moore, 1957). The habitat of this species appears to be dependent on the amount of flocculent material in the stream. If silt is absent, the fish is found in deep, slowly-moving waters, but as silting increases it changes habitat to shallow swift waters. With heavy siltation, the fish moves to riffles with large gravel and swift water (Trautman, 1957).

CHAPTER IV

FUNCTIONAL ANATOMY OF THE TELEOST BRAIN

The cyprinid fish brain, viewed from a dorsal aspect, exhibits paired forebrain lobes, paired optic lobes with longitudinal tori, a median corpus cerebellum, a single facial lobe and paired vagal lobes (Fig. 1). The valvula cerebellum, an anterior forward projection from the cerebellar base, lies in the third ventricle below the optic tecta. Hereafter in this paper, the valvula cerebellum will be referred to as the valvula and the corpus cerebellum as the cerebellum. These structures are individually or collectively associated with the basic modalities of smell, sight, equilibrium, hearing and taste. Size and degree of development of some brain lobes result from hyperdevelopment of a single sensory system, while others are correlative centers involving more than one sensory system (Schnitzlein, 1964).

In sharks and rays, where olfaction is the principal mode of obtaining food, size of the forebrain lobes is primarily dependent on the degree of elaboration of the olfactory apparatus (Aronson, 1963). Some teleosts also show pronounced enlargement of the forebrain lobes; however, the olfactory system is no longer the dominant influence. In these forms, the anterior area influenced by the olfactory system remains small while the posterior portion of the forebrain becomes greatly enlarged. According to Aronson (1963), the enlarged area is related to the hypothalamus and possibly to the thalamus with intimate connections to both structures. Association of the forebrain to higher correlative centers of the brain creates a major obstacle in attempts to correlate forebrains with types of feeding behavior. Experimental investigators have found the forebrain to function in olfaction and in formation and performance of learned responses (Hale, 1956; Janzen, 1933). Furthermore, differences in forebrain configuration may be attributed partially to available space in the cranial cavity. Miller and Evans (1965) showed that the forebrain lobes of young suckers were long and thin but as space between the eyes increased, the lobes became proportionally wider and shorter.

Optic lobe development is correlated with functional use of the visual apparatus. Herrick (1903) and Moore (1950) indicated that fishes with well-developed cutaneous sense organs in darkened habitats often show degeneration of visual capacities. Such degeneration may involve either functional or actual structural degeneration of the visual apparatus. In general, fishes inhabiting darkened environments possess smaller eyes than closely-related forms in clear-water habitats. However, not all fishes inhabiting darkened environments are characterized by small eyes. Moore (1950) pointed out that Hiodon alosoides has large eyes and probably possesses some mechanism for concentrating light. Moore and McDougal (1949) found that H. alosoides has a highly developed tapetum lucidum. Reduction of the optic lobes can usually be correlated with reduction in eye size.

The precise function of the longitudinal torus is unknown, although Franz (1912) pointed to strong torus development in fishes with good visual acuity and poor development in the blind fish, Amblyopsis spelaea. Ohta (1959) showed that the size and degree of development of the torus could not always be correlated with the size of the tectum, which to him indicated some functional dissimilarity. He indicated that the torus may "... serve to integrate photostatic and gravistatic processes."

The function of the valvula has not been clearly demonstrated. Herrick (1891) related the valvula to the active habits of the fish, while Evans (1931) noted that fishes with large facial lobes also had large valvulae. Both Franz (1911b) and Banarescu (1957) attributed increased size of the valvula to increased gustatory development. Addison (1923) and Schnitzlein (1964) demonstrated that impulses relayed over the lateral-line nerve reached the valvula, and Svetovidov (1953) showed that extirpation of the valvula in Carassius auratus caused disruptions of locomotor acts and sensory functions associated with the lateral-line organs and vision. Compensation for these disruptions was obtained after varying lengths of time. Aronson (1963) summarized the valvula function as "... part of a special mechanism for orientation through integration of vibratory and electrical sensations."

The cerebellum has been postulated as the regulatory apparatus for coordination of movements. Kurepina and Pavlovsky (1946) showed that free-swimming fishes have large cerebella and bottom-dwelling forms have small ones. Kirka (1963) suggested a close correlation between habitat selection within a stream and development of the cerebellum. He showed that fishes in the genus Aspro which live in swift currents have an enlarged, backward projecting cerebellum, while fishes in the genus Romanichthys which live under rocks in swift streams have a small cerebellum. The same type of correlation between habitat selection and cerebellum size was noted by Evans (1952). However, experimental studies to determine the function of the cerebellum have produced contradictory results attributable to species differences in cerebellar structures and connections. Franz (1912) and Hemplemann (1926) suggested an associative function for the cerebellum, while Addison (1923) noted that in fishes, unlike mammals, the cerebellum received both proprioceptive and exteroceptive sensations. Karamian (1949) believed the exteroceptive sensations were received from the auditory and visual sensory systems and proposed the cerebellum as the primary area for establishment of temporary visual and auditory associations.

Dorsal swellings of the medulla oblongata in cyprinid fishes are associated with gustation. The seventh, ninth and tenth sensory nuclei are enlarged in fishes possessing numerous cutaneous taste buds (Bhimachar, 1937). Nerves from the cutaneous sense organs enter by the communis root of the facialis nerve (VII) and terminate in the facial lobe (lobus trigeminus, tuberculum impar or lobule median du bulbe auct.). Somatic sensory fibers of the trigeminal nerve (V) which conduct tactile sensations also terminate in the facial lobe (Herrick, 1906). Termination of both types of nerve fibers in the same lobe could allow integration of tactile and gustatory stimuli, thereby increasing the efficiency of food selection. The degree of facial lobe development appears to be dependent upon the extent of the nerve supply from cutaneous taste buds and tactile organs (Herrick, 1903b). Taste buds inside the mouth and pharyngeal cavities are innervated by the glossopharyngeal (IX) and vagus (X) nerves terminating in the vagal lobes (Herrick, 1903b).

Miller and Evans (1965) have shown a close correlation between number of taste buds on palatal organs and hyperdevelopment of vagal lobes in suckers.

CHAPTER V

SENSORY MECHANISMS AND FEEDING IN TELEOSTS

Early neuroanatomical work by Herrick (1899, 1903b, 1905) showed some of the relationships between development of brain lobes and afferent sensory systems. Herrick's findings stimulated other authors to examine the brain morphology of fishes in which feeding behavior and habitat preference were well known. Usually researchers were able to show good correlation between method of feeding and size of hindbrain lobes. Reasonable correlation was shown also between size of the optic lobes and the cerebellum and some aspects of the environment. Success in this area led to studies in which inferences were made about feeding behavior and habitat selection primarily on the basis of external brain morphology. Various authors have been able to divide fishes into groups showing correlations between brain patterns and feeding behavior (Evans, 1931, 1935, 1940; Bhimachar, 1935, 1937; Satô, 1941; Kurepina and Pavlovsky, 1946; Braginskaia, 1948; Mookerjee, Ganguly and Mookherji, 1950; Evans, 1952; Svetovidov, 1953; Povlovski, 1955; Kirka, 1963; Nikitenko, 1964, Miller and Evans, 1965). There are basic similarities in all the groupings.

Evans (1931, 1935) studied the feeding habits and habitat preferences of gadids and British cyprinids in relation to brain structure. The cyprinids were placed into three groups depending on their feeding behavior and brain patterns. In group I he placed bottom-feeding fishes with large vagal and sometimes facial lobes. Barbels were present in some of these species. Nonbarbeled, sight-feeding fishes characterized by large optic and small facial and vagal lobes were placed into group II. Fishes of group III had barbels, numerous cutaneous taste buds and enlarged facial lobes. Investigations by Evans (1935) showed that brain lobes of gadids could be correlated also with types of feeding behavior. Bhimachar (1935) separated south Indian cyprinids into sight and taste feeders. Taste feeders were subdivided into intrinsic and extrinsic tasters; intrinsic tasters actively selected food in the buccal cavity, while extrinsic tasters used taste buds on the barbels and snouts for selection of food. Studies on Indian cyprinodonts showed poorly developed gustatory systems accompanied by small vagal and facial lobes in these sight-feeding fishes (Bhimachar, 1937). Satô (1941) observed the medullae of barbeled Japanese fishes with reference to feeding habits. On the basis of hindbrain morphology, fishes were divided into three groups. Group I fishes, typified by enlarged vagal lobes, used the palatal organ to discriminate food items. Fishes of group II, characterized by enlarged facial lobes, used barbels for food selection. Sight-feeding fishes with large optic and reduced facial and vagal lobes were placed in group III. Brain patterns of 13 families of Indian fishes were observed to be correlated with feeding habits (Mookerjee, Ganguly and Mookherji, 1950). Histological studies of the medulla and topographical studies of the olfactory and optic lobes resulted in three groupings. Fishes in group I, characterized by large facial and small optic lobes, fed in middle and bottom regions using cutaneous taste buds for food selection. Group II fishes were taste and sight feeders which fed at all levels from the bottom to the surface. These fishes had well-developed optic and prominent vagal and facial lobes. In some, both vagal and facial lobes were prominent. Group III fishes, characterized by well-developed optic and reduced facial and vagal lobes, were surface feeders. Four species of American cyprinid fishes were studied by Evans (1952) and placed in three groups. Fishes of group I, characterized by large vagal and notable facial lobes, were "mouth tasters." Group II included sight-feeding fishes with large optic and small vagal and facial lobes. Large facial and reduced vagal lobes characterized the "skin tasters" of group III. Svetovidov (1953) studied the brain patterns of gadids with reference to ecology and taxonomic application. Evidence was presented to show similarity in brain patterns with relationship to and dependency upon ecological factors. Schnitzlein (1964) used ganoids and selected teleosts in attempting to review relations between morphological structures and function in parts of the nervous system. Miller and Evans (1965) working with 46 species of catostomids in 13 genera showed correlations between taste bud density on lips and size of facial lobes and between taste bud density on palatal organs and relative size of vagal lobes. They indicated that brain patterns could be used taxonomically at the family level but were more useful in predicting habitat and feeding preferences of little-known species.

Weber (1827) described and correctly interpreted the function of taste buds in the palatal organ of the carp, Cyprinus carpio. Leydig (1851) discovered terminal buds on the surface of the skin and suggested that they were merely varieties of external neuromasts. Schulze (1863) correctly interpreted the function of terminal buds as chemoreceptors. Later Schulze (1870) showed that external neuromasts could be distinguished from taste buds, because the sensory cells do not extend to the basement membrane in neuromasts as they do in taste buds. Microscopical observations revealed two distinct nuclear layers in neuromasts and a single nuclear layer in taste buds. Merkel (1880) indicated that all taste buds were supported by dermal papillae, but Herrick (1903b) found some taste buds without dermal papillae. Neuromasts were sometimes found in a dermal depression but were never found on dermal papillae. Further evidence by Herrick (1903a) showed innervation of all neuromasts by acousticolateralis nerves and taste buds by communis nerves. Histologists classify taste bud cells into two groups, long sensory cells and thick supporting or sustentacular cells (Iwai, 1963). Kolmer (1927) suggested that these types are different functional stages of one cell type. However, Beidler (1963) and De Lorenzo (1963) showed that sensory cells were continuously being replaced by mitotic division on the periphery of the taste bud.

Histological studies on barbels have been made by numerous authors (Wright, 1884; Herrick, 1901, 1903a; Olmsted, 1920; May, 1925; Satô, 1937a, 1937b, 1937c, 1937d, 1938; Satô and Kapoor, 1957; Moore, 1950; Branson, 1960). Barbels usually contain numerous taste buds, increasing in density distally (Satô, 1937d). The barbel of the sawfish, *Pristiophorus japonicus*, which is devoid of cutaneous taste buds (Satô, 1937d), is a rare exception. Baecker (in Satô and Kapoor, 1957) divided five European fishes into two groups according to barbel structure - one in which the barbel was tender and yielding and a second in which the barbel was stiff. The second group was divided into motionless and flexible subgroups. Satô (1937d) divided some fishes into two groups according to histological structure of barbels. In group I were fishes lacking cutaneous sense organs and in group II were fishes with cutaneous sense organs in the barbel. Group II was subdivided into fishes with and those without dermal cartilage rods. Satô and Kapoor (1957) later placed fishes possessing bony rods in the dermis into group III. Satô (1938) investigated *Upeneus spilurus* and demonstrated the importance of barbels in locating food. The ability of the fish to find food was hindered by removal of barbels but not by loss of sight and/or smell. This was considered good evidence that in some fishes barbels perform an important gustatory function.

Moore (1950) correlated the distribution of cutaneous sense organs with habitat selection by fishes of the genus *Hybopsis*. Observations included eye size, barbel development, and number, size and distribution of taste buds. Fishes best adapted for turbid environments had the greatest number of cutaneous sense organs.

Taste buds on the gill rakers and gill arches provide a gustatory mechanism which allows identification of food items in the pharyngeal region (Iwai, 1963). Konishi and Zotterman (1963) demonstrated a differential response by fibers of the palatine nerve to varying mechanical stimulation. Distribution of these nerve fibers throughout the area supplied with taste buds permits an integrated response from two sensory systems providing for more efficient concentration of food items.

CHAPTER VI

GENERAL MORPHOLOGY AND DISTRIBUTION OF TASTE BUDS

The apical ends of cutaneous taste buds in Hybopsis normally extend above the epidermis, presumably placing the sensory cells in a more advantageous position for receiving chemical stimuli. Conversely, taste buds in the bucco-pharyngeal cavity do not extend above the mucus lining. Taste bud length appears to be correlated with the thickness of the epidermal layer, although the dermal papillae on which the taste buds rest vary in height. Although taste buds usually have a perpendicular orientation to the epidermis, many deviations were observed. External taste bud size decreases anteroposteriad (Table I) and also ventrodorsad. Internally, taste buds are relatively constant in size in the buccal cavity and on the gill arches, but they are markedly smaller on the inner opercular surface. Taste bud size appears to increase with fish size within a species. Direct correlation between taste bud size and sensitivity is not demonstrable, although it is noted that reduction in size of taste buds is usually accompanied by reduction in density so that the entire area may be less sensitive to chemical stimulation.

Density of external taste buds declines posteriad in all species except H. gelida, and density of internal taste buds increases posteriad in all species (Table I). Taste buds are largest and most numerous in those areas most likely to encounter food items; i.e., barbels, lips, venter and gill arches.

TABLE I

MEAN EXTERNAL AND INTERNAL TASTE BUD NUMBERS WITH MEAN PROXIMAL WIDTH AND LENGTH IN *HYBOPSIS*

SPECIES	TIP OF SNOUT				ANTERIOR NASAL ROSETTE				POSTERIOR NASAL ROSETTE				POSTERIOR OF RETINA				ANTERIOR OF CEREBELLUM			
	A*	B*	C*	D*	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
SUBGENUS *EXTRARIUS*																				
H. AESTIVALIS AUSTRALIS	46.5	0.0	25.5	32.9	57.0	14.0	26.4	39.9	47.9	26.9	23.7	30.5	24.5	73.0	22.8	27.9	26.3	128.3	22.3	27.4
*H. AESTIVALIS***	43.3	0.0	26.3	31.4	67.8	4.8	27.1	34.7	43.8	15.6	22.2	31.9	30.6	77.0	21.4	27.2	26.8	130.8	20.5	28.3
*H. AESTIVALIS****	39.1	0.0	28.5	33.4	38.7	7.8	29.4	37.6	21.0	13.3	24.5	32.0	17.0	50.0	24.7	29.1	----	-----	----	----
H. AESTIVALIS TETRANEMUS	16.7	0.0	26.2	30.5	28.1	0.4	27.3	31.2	33.8	9.2	24.1	29.7	23.0	32.8	22.3	26.4	23.7	48.0	21.3	24.2
H. AESTIVALIS HYOSTOMUS	16.1	0.0	27.2	31.4	21.3	0.4	26.5	33.5	18.0	6.3	23.6	30.9	12.5	34.2	21.7	25.8	7.8	34.2	21.0	23.7
SUBGENUS *NOCOMIS*																				
H. LEPTOCEPHALA	42.0	0.0	31.6	54.0	57.5	9.8	32.0	48.8	24.4	17.7	31.2	43.6	11.8	28.5	31.6	43.6	11.7	57.4	29.6	40.8
H. (*NOCOMIS*) SP.	33.4	0.0	31.0	45.3	30.6	8.7	30.3	42.3	11.2	10.5	27.0	37.3	6.2	25.2	25.0	35.0	5.6	35.6	24.0	33.0
H. MICROPOGON	30.2	0.0	31.3	40.0	16.0	5.6	31.3	40.7	11.3	7.7	30.0	35.0	7.5	28.0	26.7	34.7	8.1	42.2	26.0	34.0
H. BIGUTTATA	30.0	0.1	35.0	52.0	18.3	8.1	30.3	47.7	9.2	5.9	29.3	41.3	7.1	20.3	27.0	41.3	5.7	39.6	28.7	40.7
H. BELLICA	27.6	0.0	28.5	36.0	28.6	4.1	25.0	35.0	12.5	9.4	25.0	32.0	12.2	18.6	23.5	31.5	11.2	37.6	27.0	31.0
SUBGENUS *HYBOPSIS*																				
H. LABROSA	34.2	0.0	24.0	40.0	32.8	6.6	28.0	44.0	20.0	5.5	32.0	36.0	14.9	16.2	30.0	34.0	12.0	30.5	30.0	34.0
H. STORERIANA	21.8	0.0	20.0	52.0	30.9	7.4	23.0	43.0	18.0	15.6	23.0	38.0	7.2	88.8	24.0	33.0	7.0	139.2	24.0	26.0
H. RUBRIFRONS	20.5	0.0	25.0	39.0	43.0	6.2	26.0	39.0	17.8	15.7	26.0	37.0	6.2	65.9	23.0	30.0	5.6	157.9	24.0	28.0
H. AMBLOPS	18.0	0.0	24.8	40.0	22.2	9.8	25.1	38.8	7.5	11.1	24.0	33.1	2.6	64.1	21.0	31.0	2.2	125.1	19.5	28.8
H. HYPSINOTA	11.0	0.0	28.0	42.0	45.8	4.0	30.0	46.0	17.4	15.8	30.0	44.0	12.2	101.2	24.0	36.0	9.6	120.0	22.0	33.0
SUBGENUS *ERIMYSTAX*																				
H. X-PUNCTATA	31.5	0.2	31.5	52.0	33.4	6.2	30.5	48.0	14.6	5.5	24.0	35.0	7.8	17.8	25.5	33.0	5.3	34.6	24.7	30.7
H. HARPERI	18.8	0.0	27.0	42.2	16.5	8.4	25.5	36.8	5.5	7.2	24.8	35.5	4.1	15.8	23.5	34.0	4.0	29.5	24.2	32.5
H. DISSIMILIS	14.8	0.0	30.0	35.5	17.0	2.4	30.5	43.0	7.0	4.2	34.5	36.5	6.9	13.6	26.5	35.0	5.0	22.2	33.0	39.0
H. INSIGNIS	14.1	0.0	33.0	42.7	29.6	3.3	34.7	54.0	12.8	5.4	29.7	40.7	5.8	23.7	30.3	28.3	5.7	27.9	32.3	36.7
H. CAHNI	13.3	0.0	32.0	52.0	9.6	4.7	60.0	68.0	6.5	3.8	40.0	60.0	5.0	20.6	25.0	30.0	1.5	20.0	24.0	30.0
SUBGENUS *MACRHYBOPSIS*																				
H. MEEKI	33.1	0.0	23.7	35.4	36.6	7.5	27.4	36.0	19.9	12.8	28.0	34.0	14.6	41.2	28.3	36.8	10.6	64.4	26.6	36.6
H. GELIDA	56.1	0.0	31.0	41.0	53.1	6.2	34.0	38.0	56.1	8.9	36.0	40.0	52.8	22.3	26.0	36.0	47.4	36.1	32.0	44.0
SUBGENUS *PLATYGOBIO*																				
H. GRACILIS	41.0	1.2	31.6	44.6	31.8	13.3	31.2	43.6	26.1	12.3	30.5	42.0	15.4	24.3	31.0	43.0	18.4	53.6	28.5	41.0
SUBGENUS *COUESIUS*																				
H. PLUMBEA	12.5	1.4	31.2	41.4	10.3	5.2	28.4	42.4	5.4	4.6	29.2	38.4	4.3	10.3	30.4	40.8	3.9	22.1	24.4	37.6
SUBGENUS *OREGONICHTHYS*																				
H. CRAMERI	13.4	0.0	28.0	38.0	11.6	4.2	24.0	37.0	4.1	6.1	25.0	29.0	2.3	14.2	22.0	31.0	2.6	22.4	22.0	29.0

* A = EXTERNAL TASTE BUDS/SECTION, B = INTERNAL TASTE BUDS/SECTION, C = PROXIMAL WIDTH IN MICRONS, D = LENGTH IN MICRONS

** PECOS RIVER FORM

*** NINNESCAH RIVER FORM

Most Hybopsis species have large compound taste buds in the first interradial membranes of the pectoral fins (Table II). Compound taste buds are, however, distributed in other interradial membranes of species which inhabit turbid water; i.e., H. aestivalis, H. gelida, H. gracilis, H. meeki, and H. storeriana. Silty-water forms have more compound taste buds than clear-water cognates as demonstrated by Moore (1950) in H. gracilis. The protuberences formed by these taste buds may be distinguished from breeding tubercles by their distribution on the fin. Tubercles occur on principal fin rays in two or three rows which branch with the fin ray as in Notropis lutrensis (Koehn, 1965), while taste buds are located on the interradial membranes.

The histological structure of barbels in Hybopsis is uniform except in taste bud quantity and epidermal thickness (Table II). Barbels of all species are the fleshy, pendant type with no evidence of osseous, cartilaginous or muscular supporting components. Taste bud density increases distally in all species.

The mean number of taste buds per section increases with fish size (Figs. 2, 3). If all taste buds were formed simultaneously during the initial period of growth and histological differentiation, gradual reduction in taste bud number per section would occur as size of the fish increases. However, there is an increase in taste buds per section with increased size. Therefore, new taste buds must be added during the growth of the fish. Concerning compound taste buds in the first interradial membranes of H. gracilis, Moore (1950) noted that "... numbers of these organs are obviously greater in old fish than younger ones." Increase in the number of sensory elements may be a fairly general phenomenon since Allis (1888) indicated that the number of lateral-line pores on the head of the bowfin, *Amia calva*, apparently increases with age.

TABLE II

NUMBER AND SIZE OF TASTE BUDS ON BARBELS AND THE PRESENCE OR ABSENCE OF COMPOUND TASTE BUDS ON PECTORAL FINS OF *HYBOPSIS*

Species	On Barbels			Compound Taste Buds* on Pectoral Fins
	Number	Width (μ)	Length (μ)	
H. aestivalis	6-12	22-30	24-34	+
H. meeki	6-10	18-28	20-30	+
H. gelida	8-11	24-30	40-44	+
H. gracilis	3-5	28-40	48-60	+
H. storeriana	1-4	30-40	38-50	+
H. amblops	0-2	20-26	24-28	-
H. labrosa	1-3	26-32	24-28	+
H. hypsinota	1-4	28-30	45-50	-
H. rubrifrons	1-3	26-30	42-48	-
H. cahni	0-2	24-28	32-36	+
H. dissimilis	0-1	34-38	48-56	+
H. harperi	0-1	26-36	28-34	-
H. insignis	1-3	28-32	30-36	+
H. x-punctata	0-2	38-44	56-104	+
H. bellica	1-3	24-30	28-34	+
H. biguttata	1-3	30-44	56-60	+
H. micropogon	1-3	40-52	56-60	+
H. (*Nocomis*) sp.	1-2	26-32	38-40	+
H. leptocephala	1-3	26-28	45-50	+
H. crameri	0-2	24-26	24-32	-
H. plumbea	1-2	36-44	52-60	+

*+ indicates presence of compound taste buds in the first inter-radial membrane, - indicates absence or extreme size reduction of compound taste buds

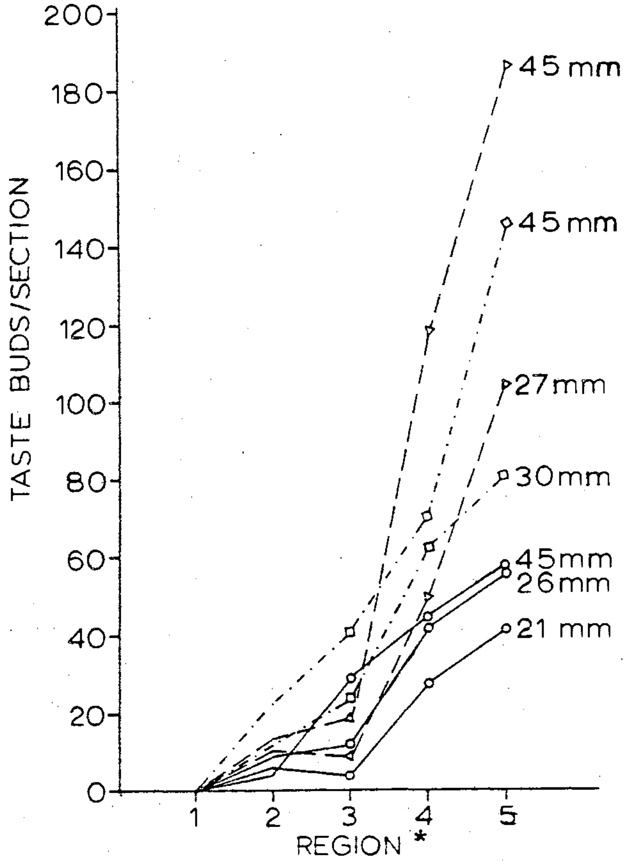

Fig. 2. Comparison of Numbers of Internal Taste Buds in Different Body Regions of Three Species of Hybopsis. △ = H. amblops, ◇ = H. aestivalis, ○ = H. meeki

*1 = snout, 2 = anterior rosette, 3 = posterior rosette, 4 = posterior retina, 5 = anterior cerebellum

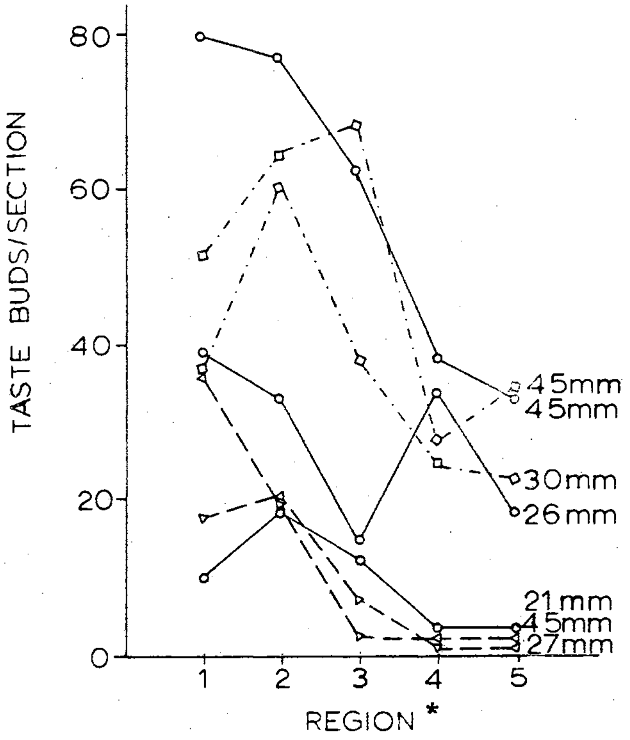

Fig. 3. Comparison of Numbers of External Taste Buds in Different Body Regions of Three Species of Hybopsis. △ = H. amblops, ◇ = H. aestivalis, ○ = H. meeki

*Refer to Fig. 2 for region code

CHAPTER VII

MORPHOLOGY OF BRAIN LOBES IN *HYBOPSIS*

Since the brain develops earlier than most other parts of the vertebrate body (Arey, 1954), it is relatively larger in small fish (Fig. 4). In agreement with Geiger's (1956a, 1956b) findings in European fishes, data in the present study appear to indicate allometric growth of brain lobes. Presumably, the brain pattern may be used to determine prominent sensory modalities at any developmental stage.

Evaluations based on topographic views of fish brains permit reasonably accurate predictions of feeding habits and some aspects of habitat preferences of many fishes. However, predictions based on a topographic view of the vagal lobes in *Hybopsis* are probably inaccurate. The vagal lobes, viewed from above, appear excessively enlarged in only one species, *H. hypsinota* (Fig. 22). Actually, the lobes are enlarged in several species but the enlargement is concentrated ventrolaterally. Although precise measurement and visual representation are impossible, microscopic examination of vagal lobe cross-sections reveals their correct size and configuration.

The longitudinal tori are structures of dubious function located between or beneath the optic tecta. They are not externally visible in all species of *Hybopsis*. In sight-feeding forms, cylindrical tori are concealed beneath the optic tecta at the midline (Fig. 5). With

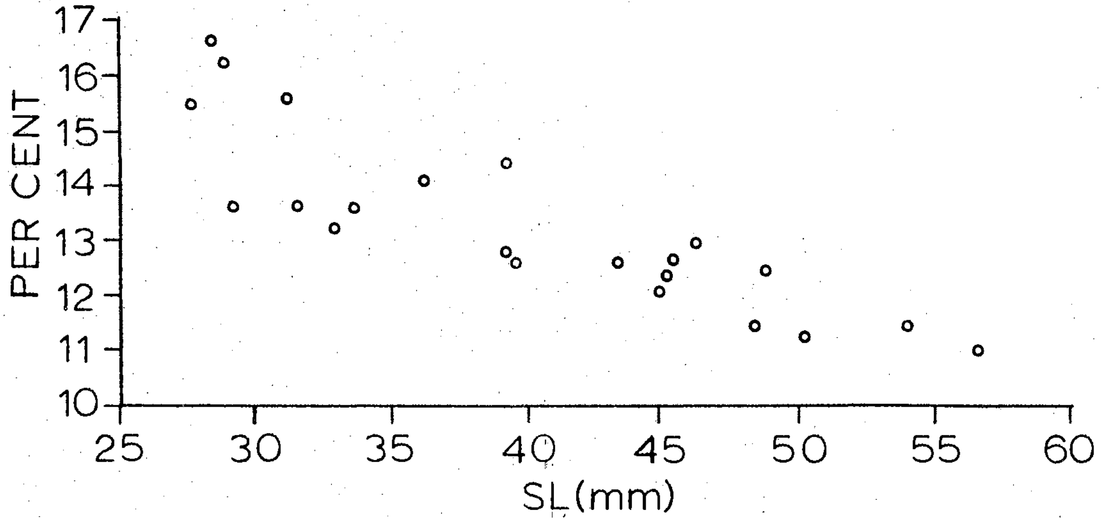

Fig. 4. Total Brain Length Expressed as Per Cent of Standard Length in Hybopsis aestivalis.

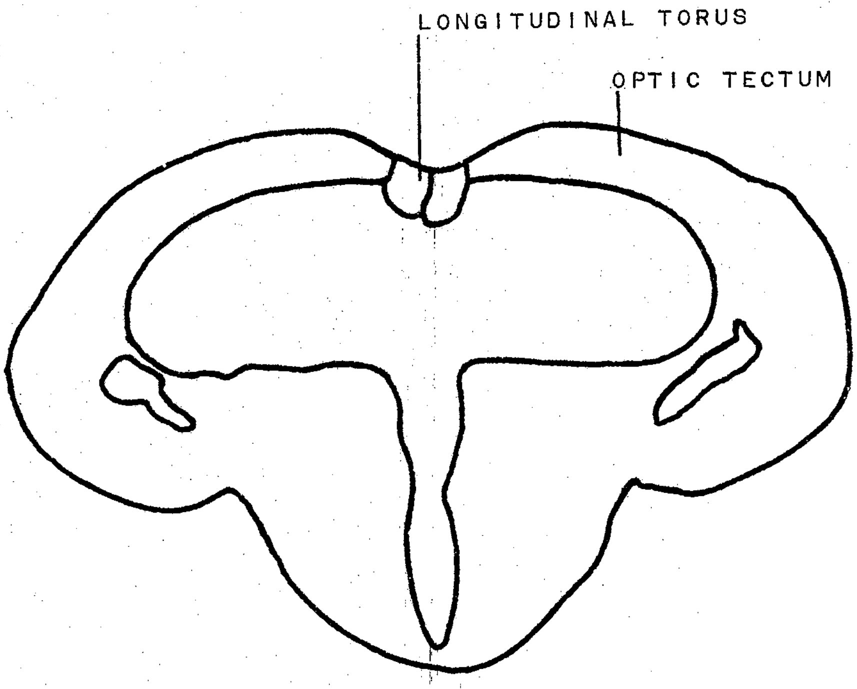

Fig. 5. Cross-section of the Brain to Show the Longitudinal Tori in Hybopsis crameri.

reduction of the optic tectum, the tori become flattened, laterally expanded and exposed to external view (Figs. 6, 7). The degree of distortion is greatest in those fishes with the greatest cutaneous gustatory development; i.e., H. aestivalis, H. gelida and H. meeki. It is not immediately evident whether change of size accompanies change in shape, although the total cross-sectional area appears to be less in the flattened tori. The extent of exposure of the tori is indicative of the development of the valvula. Fishes with extremely flattened tori also possess an enlarged valvula. Although larval or post-larval fishes were not examined, it is probable that hyperdevelopment of the valvula during growth pushes the optic lobes aside and exerts pressure on the tori.

Size-configurational variation of brain lobes within a species increases as the habitat becomes more variable. Optic lobe width (Fig. 8) was selected to represent this variability, although similar variability can be shown in other brain lobes. For example, H. aestivalis inhabits both clear and turbid habitats, and exhibits more variability than inhabitants of constant environments such as H. harperi which lives in clear, spring-fed streams (Fig. 8). These data also suggest that width rather than length measurements are better indicators of habitat preference. This is probably so because any longitudinal enlargement tends to displace adjacent brain lobes while lateral expansion usually is prevented only by available cranial space. However, there are lobes which can expand longitudinally without displacing adjacent lobes. The cerebellum can extend posteriad, overlapping the facial lobe, while the valvula can extend anteriad into the third ventricle. Forebrain lobes may also be lengthened anteriad.

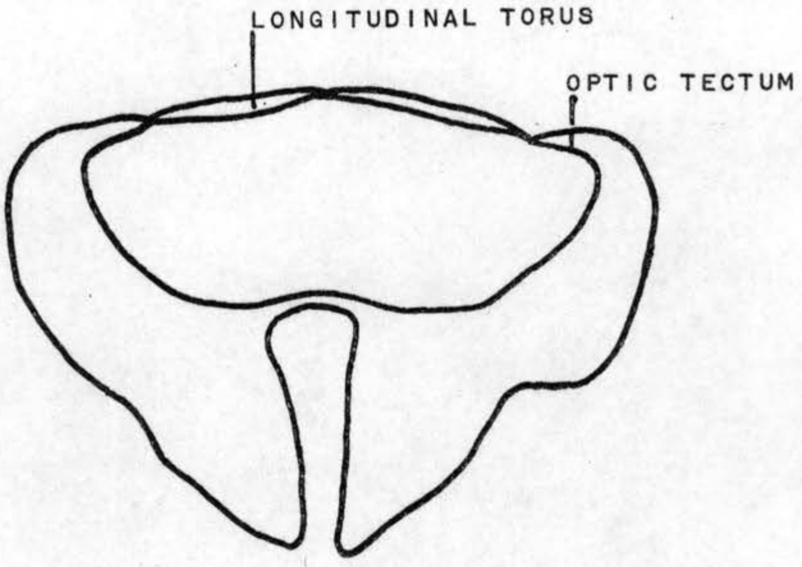

Fig. 6. Cross-section of the Brain to Show the Longitudinal Tori in Hybopsis meeki

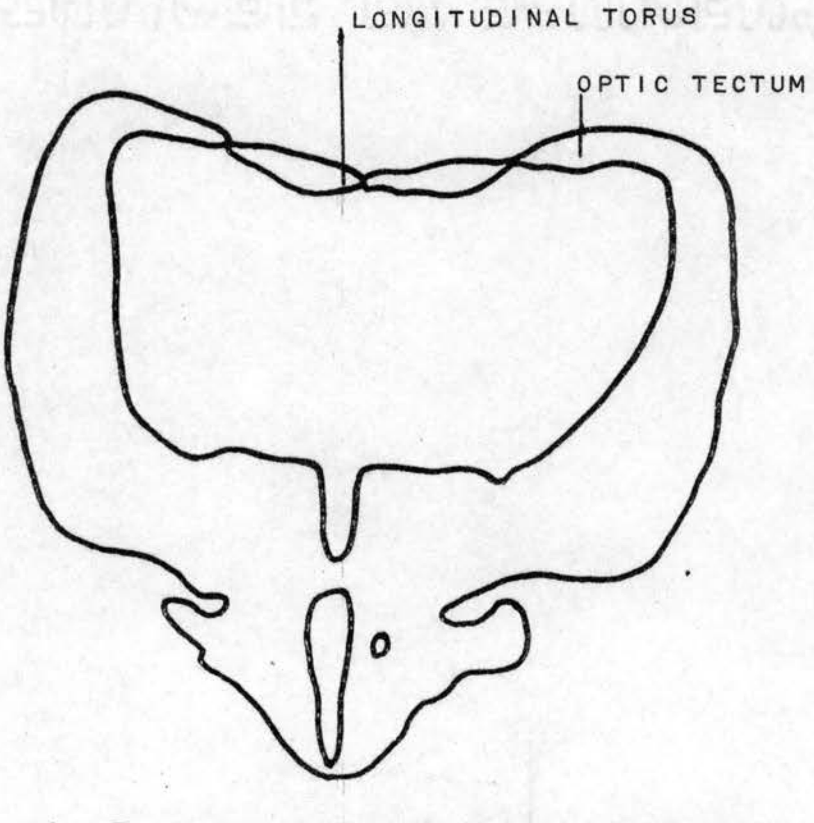

Fig. 7. Cross-section of the Brain to Show the Longitudinal Tori in Hybopsis labrosa

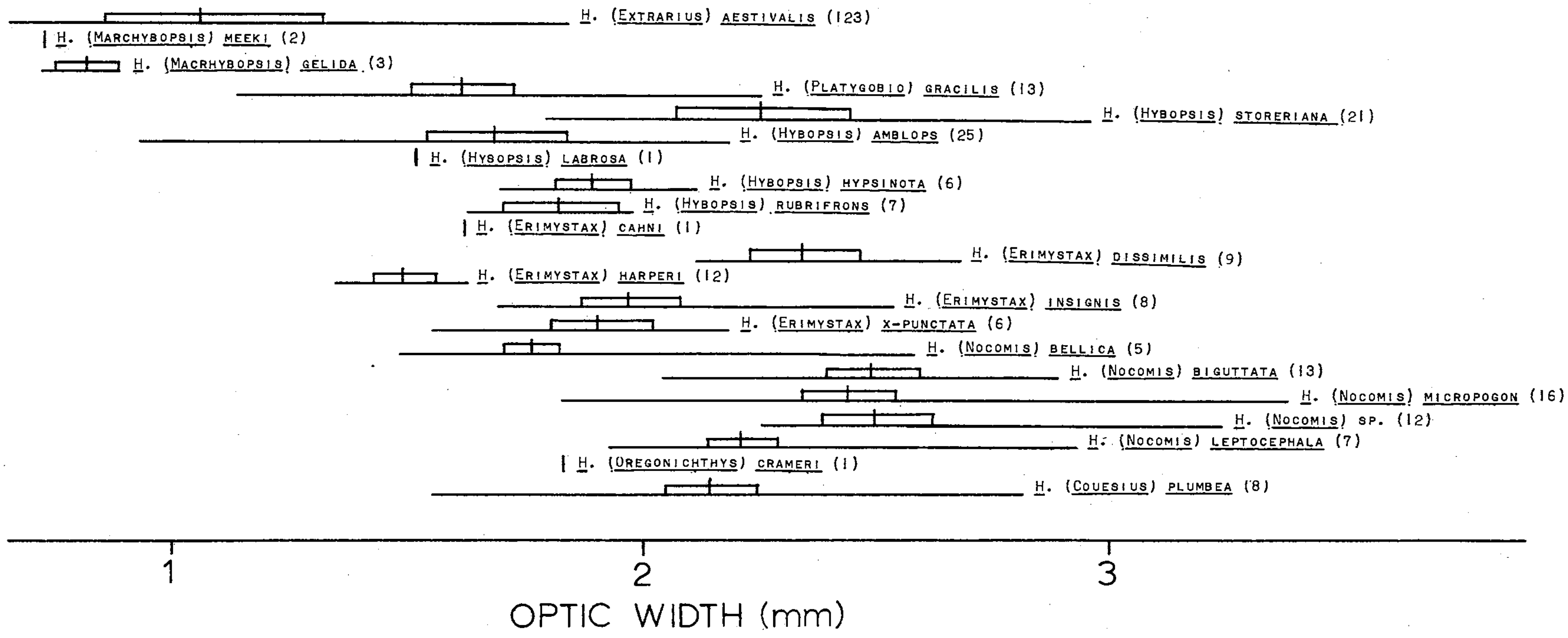

Fig. 8. Variability of optic lobe width adjusted for the dependent variable in Hybopsis. Vertical bar = mean, horizontal line = range, open rectangle = two standard deviations, number in parentheses = sample size.

The ratio, facial width/optic width, provides an index to the relative size of these lobes in Hybopsis (Fig. 9). This index also may indicate relative usefulness of the lobes to the fish. H. aestivalis is separated into groups according to river systems to show an index shift as the water quality changes from turbid to clear. No attempt was made to specify an index value where one sensory mechanism was predominant over the other, but it was evident that fishes with high indexes were primarily taste feeders. An inverse relationship exists between the width of the optic and facial lobes, when considered as a per cent of total brain length (Table III). This inverse correlation tends to break down in the subgenus Hybopsis.

TABLE III

MEAN FACIAL AND OPTIC LOBE WIDTH EXPRESSED AS PER CENT OF TOTAL BRAIN LENGTH IN HYBOPSIS

Species	Facial	Optic
H. gelida	22.7	12.3
H. meeki	18.5	13.2
H. insignis	17.0	27.4
H. aestivalis	16.6	18.6
H. gracilis	14.9	22.8
H. x-punctata	14.5	27.4
H. labrosa	14.2	22.4
H. leptocephala	13.4	29.8
H. bellica	13.3	27.2
H. dissimilis	13.0	28.1
H. storeriana	12.9	24.7
H. cahni	12.9	24.7
H. (Nocomis)	12.4	28.9
H. plumbea	11.8	27.4
H. micropogon	10.8	28.0
H. biguttata	10.6	28.8
H. crameri	10.5	30.2
H. rubrifrons	10.3	23.4
H. harperi	8.8	24.1
H. amblops	7.8	23.8
H. hypsinota	6.7	27.4

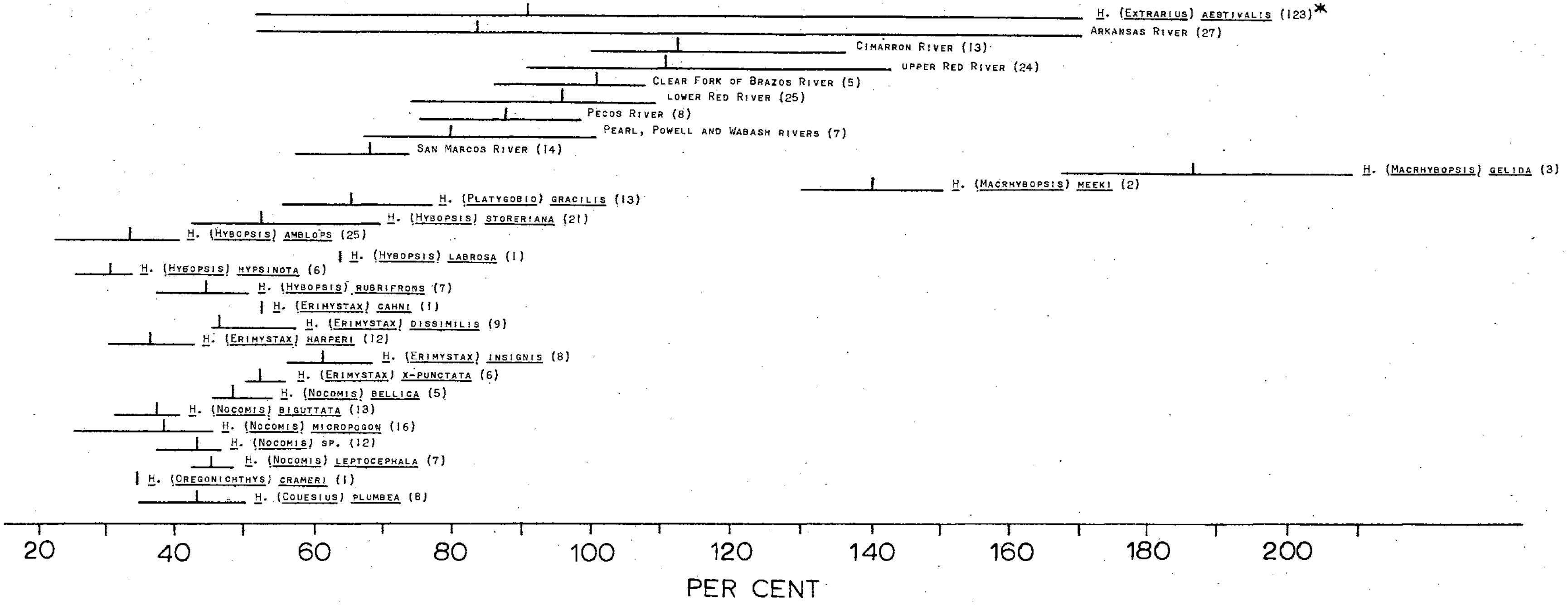

Fig. 9. Facial lobe width expressed as a per cent of optic lobe width in Hybopsis. Vertical bar = mean, horizontal line = range, number in parentheses = sample size.

* H. aestivalis is separated into river systems.

CHAPTER VIII

SYSTEMATIC REVIEW

Subgenus *Extrarius*

The subgenus consists of a single species composed of six nominal subspecies: *Hybopsis aestivalis aestivalis* (Girard) of clear Rio Grande tributaries, *H. a. hyostomus* (Gilbert) of streams east of the Mississippi River, *H. a. marconis* (Gilbert) of the San Marcos River, *H. a. sterletus* (Cope) of the Rio Grande proper, *H. a. tetranemus* (Gilbert) of the Arkansas River and *H. a. australis* (Hubbs and Ortenburger) of the Red River. For convenience, names of the nominal subspecies will be used when the geographic location of a specimen corresponds with that designated for a nominal subspecies. This should not be interpreted as support for or recognition of the nominal subspecies, since sufficient material was not available for a systematic review.

Morphology: *H. aestivalis* is adapted for bottom dwelling by possessing a depressed body, elongate snout, subterminal mouth, well developed barbels and large pectoral fins. It exhibits more morphological plasticity than any other species in the genus *Hybopsis*, probably because of its highly variable habitat preferences.

In general, the number and length of barbels are correlated with eye size and habitat (Moore, 1950). Large eyed forms, *H. a. hyostomus*, *H. a. marconis* and *H. a. aestivalis*, inhabit clear waters and possess a single pair of relatively short barbels. Small eyed forms, *H. a. tetranemus* and *H. a. australis*, inhabit turbid waters and may have one or two pairs of barbels. *H. a. australis* in the upper Red River always has two pairs of long barbels. Specimens are sometimes found with supernumerary barbels. Hubbs and Ortenburger (1929) found one specimen with seven barbels on one side. The summed barbel length of a four-barbeled specimen may exceed 15 mm. Subspecies in the lower Red and Arkansas River systems have one or two pairs of barbels, often with one well developed and one rudimentary pair. Hubbs and Ortenburger (1929) suggested that barbel development was a recent compensatory adaptation for reduced vision in turbid habitats.

Pectoral fins are large expansive structures in all *H. aestivalis*. Compound taste buds are usually restricted to the first interradial membranes of clear-water forms but scattered through other interradials of silty-water forms. In a bottom-dwelling fish, perhaps deprived of effective vision, chemoreceptors on the pectoral fins would greatly increase the sensory area and thus increase the efficiency of energy expenditure during food searching behavior. However, chemoreceptors are found on the pectoral fins of fishes other than strictly bottom-feeding forms (Table III).

Brain pattern: Forebrain lobes in *H. aestivalis* (Figs. 10-14) are moderately well developed except in the Pecos River form. Specimens from this area exhibit enlarged, laterally expanded lobes with prominent dorsal swellings (Fig. 14). Optic lobes are highly variable in size and configuration. An increase in the optic lobe size occurs in the following order: *H. a. australis*, *H. a. tetranemus*, (Pecos River form), *H. a. hyostomus* and *H. a. marconis*. Longitudinal tori are connected

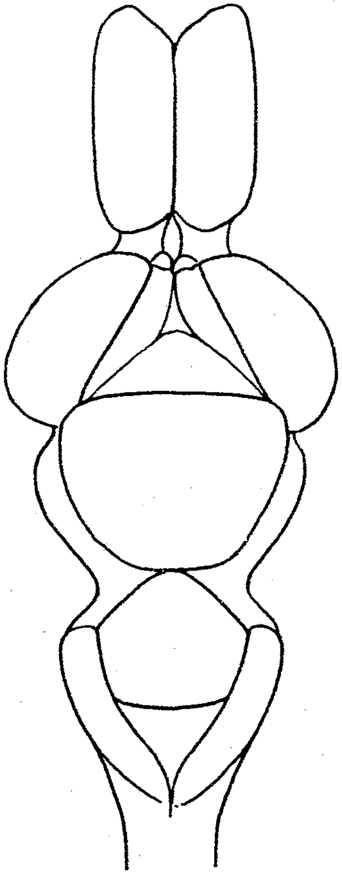

Fig. 10. Brain Pattern in *Hybopsis aestivalis australis*

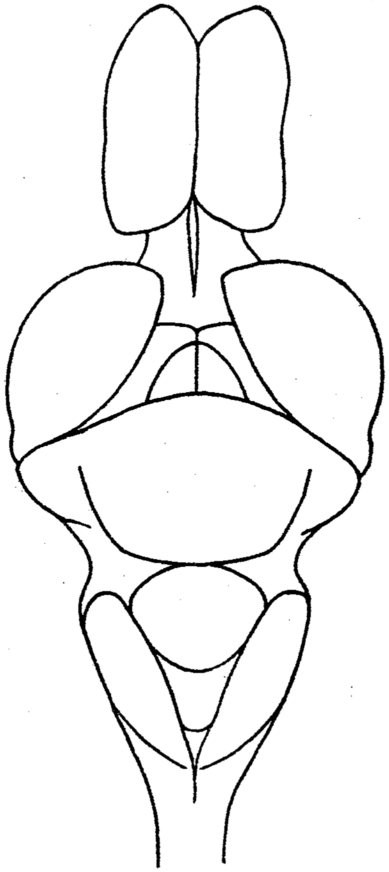

Fig. 11. Brain Pattern in *Hybopsis aestivalis tetranemus*

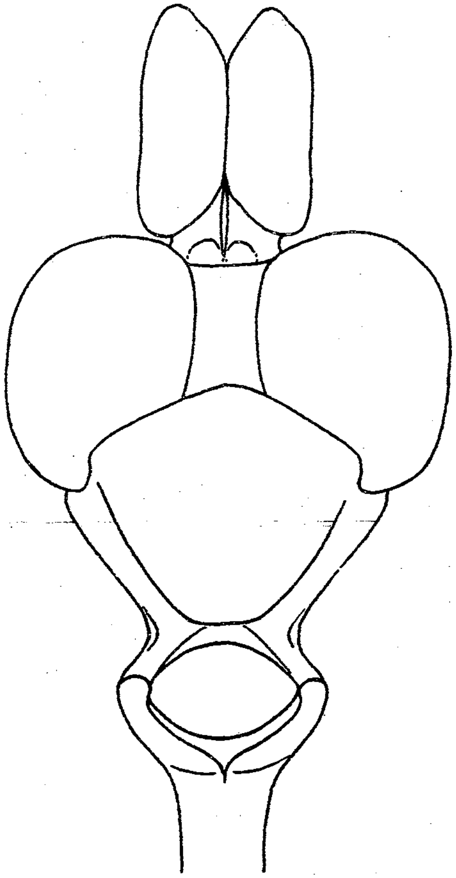

Fig. 12. Brain Pattern in *Hybopsis aestivalis marconis*

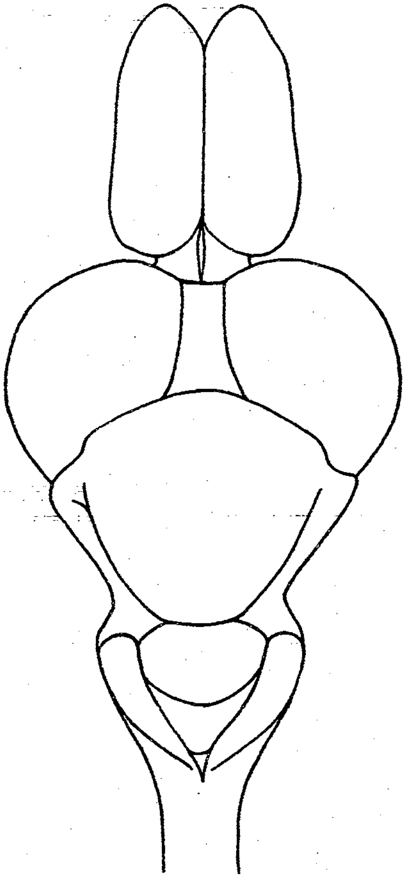

Fig. 13. Brain Pattern in *Hybopsis aestivalis hyostomus*

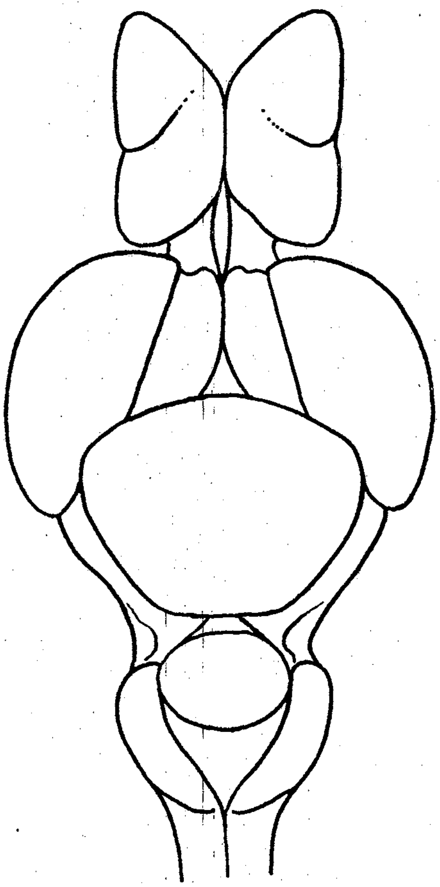

Fig. 14. Brain Pattern in Hybopsis aestivalis (Pecos River Form)

along their entire length in H. a. hyostomus and H. a. marconis but are separated posteriad in other forms. This separation is correlated with an increased size of the valvula and/or reduction of the optic lobes. The size and position of the optic lobes, longitudinal torus and valvula appear to be functionally related. In forms with large optic lobes, the torus is narrow and the valvula is small, while forms with small optic lobes have a broad torus and a large valvula. The cerebellum is well developed, though variable in configuration in the forms observed.

The corpus is slightly larger than a single optic lobe and fairly constant within a particular form. The prominent feature of the hindbrain is the extreme enlargement of the facial lobe. Facial lobe size is usually inversely correlated with optic lobe size. Vagal lobes are moderate to well developed. In H. a. marconis the vagal lobes flare laterally, causing a reduction in the size of the rhomboid fossa; other forms have longer vagal lobes with pronounced rhomboid fossae.

Discussion: Since the size of the post-diencephalic brain is closely related to the development of several sensory modalities, it should be possible to relate gross variations in brain morphology to specific sensory and possibly behavioral specializations in H. aestivalis. Populations of this species inhabit lotic waters with an extremely wide range of turbidity characteristics. Moore (1950) demonstrated that fishes inhabiting highly turbid waters of Great Plains rivers had smaller eyes and compensatory hyperdevelopment of cutaneous sense organs. The following discussion will therefore investigate relationships between environmental conditions and development of afferent sensory systems and central nervous system correlates.

Streams of the Great Plains are subject to extreme changes in flow and turbidity (Table IV). Turbidity levels within a river basin vary depending on the location in the basin and tend toward more constant, lower average levels in the lower reaches, at least in the Arkansas River (Table IV). According to Moore (1950), the Red River in the past carried a greater silt load than the Arkansas River. As might be expected, the optic lobes of H. a. australis are smaller than those of H. a. tetranemus. Subpopulations of H. aestivalis in the Arkansas River appear to have become adapted to slightly different conditions.

This is illustrated by H. aestivalis from the lower Arkansas River having larger optic lobes than upper Arkansas River forms. Optic lobes of the Pecos River form are larger than in the preceding forms. Although data for the Pecos River were not available, it is probable that turbidity would be lower than in the Arkansas or Red rivers. Eyes and optic lobes of H. a. marconis and H. a. hyostomus are approximately the same size; both being larger than preceding forms. The turbidity in the Wabash River, where H. a. hyostomus is an inhabitant, is much lower than in streams of the Great Plains (5-480 Jackson units, mean 70.4, Indiana State Board of Health, 1963). Similarity in the optic lobes of H. a. marconis and H. a. hyostomus would also indicate a similar turbidity level in their habitats. Basic similarities in the brain patterns of H. a. marconis and H. a. hyostomus suggest either similar ecological conditions or an extremely close phylogenetic relationship. H. a. hyostomus is found east of the Mississippi River and H. a. marconis is confined to a few rivers in south Texas. Because of the wide geographic gap between these two forms, similarities of body and brain pattern are probably attributable to convergent adaptation caused by similar selection pressures. The cerebellum of both forms is elongated posteriad more than in other forms. This posterior elongation overlaps the facial lobe in H. a. hyostomus. Kirka (1963) related the enlarged posteriorly projecting cerebellum to life in swift waters. While all H. aestivalis inhabit moderate to swift waters, it is suspected that H. a. marconis and H. a. hyostomus reside in swifter waters than other forms.

TABLE IV

RANGES OF TURBIDITY AND FLOW FOR THE YEARS 1961-62 IN THE ARKANSAS RIVER*

Station	Turbidity (Jackson Units)	Flow (cfs)
Coolidge, Kansas**	25-5000(622.5)***	3-286
Ponca City, Oklahoma	25-2000(293.7)	1750-94500
Pendleton Ferry, Arkansas	144-620 (272.7)	6100-104000

*U. S. Dept. of Health, Education and Welfare, 1962

**Stations listed from upper to lower reaches

***Mean annual turbidity

In H. aestivalis with reduced optic lobes and eyes, there has been a compensatory increase in the number of cutaneous taste buds (Table V). Development of supernumerary or elongate barbels provides greater surface for cutaneous taste buds. A conservative estimate of 2000 taste buds on the barbels of an H. a. australis illustrates the extreme sensitivity and probable utility of the barbels. Numerous ridges and papillae are also present on the isthmus region of H. aestivalis from turbid streams. The tips of these structures are profusely supplied with taste buds. Obviously, fishes possessing abundant cutaneous taste buds occupy an advantageous feeding position over other fishes during times of extreme turbidity when vision may not be effective.

The facial lobe width, expressed as a percentage of optic lobe width, is greater in turbid-water forms of H. aestivalis (Fig. 8), reflecting an increase in numbers of cutaneous taste buds (Table V). Density of internal taste buds is also positively correlated with increased turbidity (Table V) which is reflected in the relative size of the vagal lobes.

TABLE V

MEAN EXTERNAL AND INTERNAL TASTE BUDS PER SECTION FROM FIVE REGIONS IN *HYBOPSIS AESTIVALIS*, SUBGENUS *EXTRARIUS*

Region*		*H. a. australis*	*H. a.* (Pecos River)	*H. a.* (Ninnescah River)	*H. a. tetranemus*	*H. a. hyostomus*
1	A	45.6	43.4	39.1	16.7	16.3
	B	0.0	0.0	0.0	0.0	0.0
2	A	56.9	67.8	38.9	28.1	21.3
	B	13.9	4.8	7.8	0.4	0.4
3	A	42.9	43.8	21.0	33.8	18.0
	B	26.9	15.6	13.3	9.2	6.3
4	A	24.5	30.6	17.0	23.0	12.5
	B	73.0	77.0	50.0	32.8	21.7
5	A	26.3	26.8	----	23.7	7.7
	B	128.3	130.8	----	49.8	34.1

*1 = tip of snout, 2 = anterior of nasal rosette including the lips, 3 = posterior of nasal rosette, 4 = posterior of retina, 5 = anterior of cerebellum, A = number of external taste buds, B = number of internal taste buds

Methods of securing food must vary with the habitat and efficacy of receptors. Fishes in turbid environments rely primarily on an abundance of cutaneous taste buds for location of food, while those in clear waters probably depend more on visual sensitivity. The Pecos River form could possibly be an exception. Olfaction in these fishes may play an important role in securing food. However, the Pecos River form has a cutaneous taste bud density equivalent to that of the taste-feeding *H. a. australis*.

Once food has been located and ingested, nutritive items must be separated from nonnutritive material in the bucco-pharyngeal cavity. Longitudinal folds in the top of the buccal cavity originate just inside the lips and extend into the pharyngeal region. Taste buds are located at intervals along the apices of the folds. Connective tissue supporting the mucosa lining the folds is interspersed with scattered bundles of striated muscle which may permit a manipulative function for these folds. In the pharyngeal region the muscle bundles form a thick network above and to either side of the gill arches. In some respects this area resembles the palatal organ found in catostomids, although it is not as well developed. This muscle mass may possibly be activated by chemical and/or tactile stimuli to aid in the selection and concentration of food. The possible sorting function of the longitudinal folds may be facilitated by action of the gill arches and gill rakers.

Extrarius, with reduced optic lobes and numerous cutaneous taste buds, also has numerous taste buds in the pharyngeal region. Furthermore, fishes with well developed optic lobes and few cutaneous taste buds have few internal taste buds (Table V). It seems plausible that sight-feeding fishes would be better able than taste-feeding fishes to locate a specific food item in the environment. Taste-feeding fishes would be able to locate feeding areas but possibly could not select specific food items. It seems likely that if a fish is able to locate food items visually, the amount of extraneous detritus ingested would be low and the amount of separation necessary in the buccal cavity minimal. Conversely, if taste-feeding fishes are not able to locate a single food item, they probably ingest greater quantities of detritus and must have large numbers of internal taste buds for efficient food sorting.

Behavioral observations of *Hybopsis aestivalis australis* and *H. a. tetranemus* correspond closely with behavior predicted on the basis of gross morphology and histological observations, although laboratory conditions differed from those in nature in that no current was present and the water was kept clear for observational convenience. No behavioral differences were detected between the observed subspecies. Fish swam slowly with pectoral fins spread widely and barbels in contact with the sand. Occasionally, they would stop and turn to pick up materials from the bottom. It seems likely that cutaneous taste buds on the barbels, fins or body had detected the food. After a short interval, small quantities of sand were ejected from the mouth. Introduction of live *Daphnia* sp. elicited no response until the *Daphnia* touched or swam close to the fish. When dry food was introduced, no response was affected until it had sunk almost to the bottom. Usually at this point, the nearest fish would initiate a rapid searching movement with pectorals spread widely and barbels in contact with the sand. Almost immediately, other fish began the same behavior. Whether this resulted from activity of the first fish or independent detection of food is not known. When live and dry food were introduced simultaneously, fish began feeding on the dry food first, perhaps because of the rapid diffusion of strong sapid materials from the dry food. Feeding behavior in *H. a. australis* and H. a. tetranemus apparently is primarily taste oriented, although vision may play an important role in securing food close to the head. Fish were kept in aquaria for over three months with no apparent change from taste to sight feeding, even though the water was clear at all times.

Subgenus Nocomis

The subgenus Nocomis consists of five species: Hybopsis bellica, H. biguttata, H. leptocephala, H. micropogon and H. (Nocomis) sp.

Morphology: These fishes are morphologically quite similar, particularly during nonbreeding seasons. The large nuptial tubercles characteristic of males in this group are often used for species differentiation. If nuptial tubercles are present on females, they appear only as white spots in the epidermis (Lachner, 1952). The body configuration shows little modification for a specific habitat-type. Barbels of Nocomis are conspicuous structures, but due to the paucity of taste buds, it is doubtful that they are of great utility in locating food. Although the eyes are not particularly large, Nocomis apparently has well developed visual acuity as shown by the ability to construct elaborate nests (Reighard, 1943), and by the ability to locate food visually.

Brain pattern: Brain patterns of the species in the subgenus Nocomis show many basic similarities (Figs. 15-19). Forebrain lobes of H. leptocephala and H. (Nocomis) sp. are nearer to the optic lobes than in the other three species. Size and shape of the forebrain lobes are approximately the same, except in H. (Nocomis) sp. where they are larger and have a different configuration. The large round optic lobes join

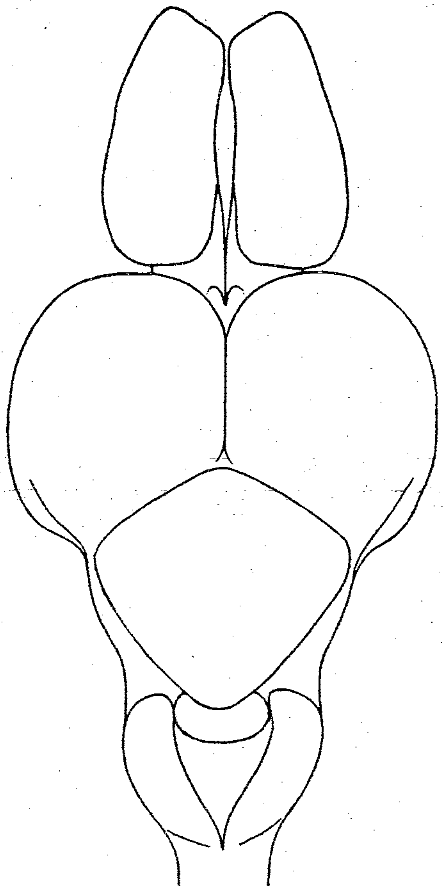

Fig. 15. Brain Pattern in Hybopsis (Nocomis) Sp.

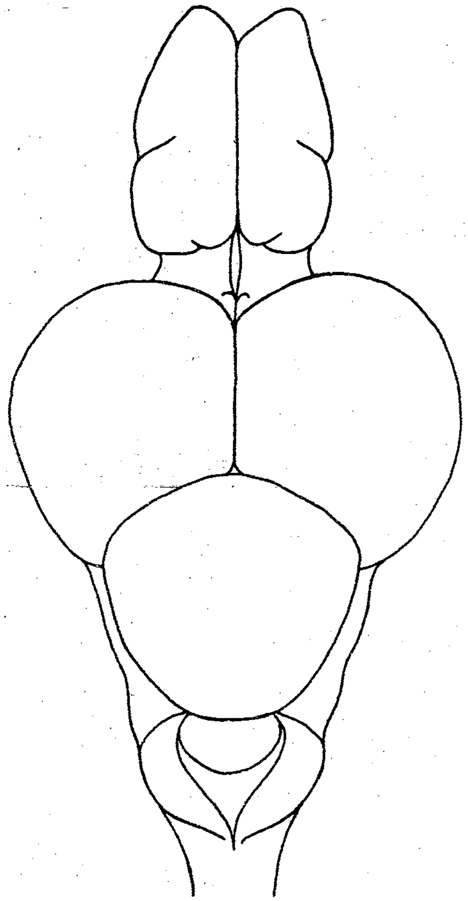

Fig. 16. Brain Pattern in Hybopsis micropogon

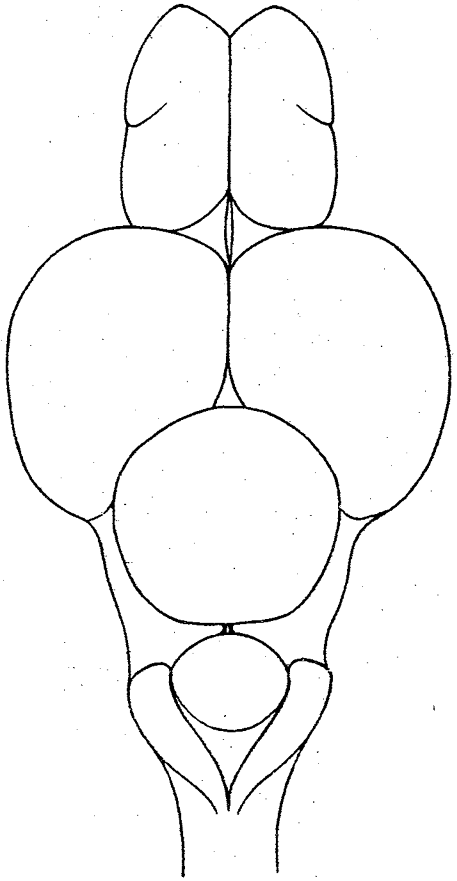

Fig. 17. Brain Pattern in Hybopsis leptocephala

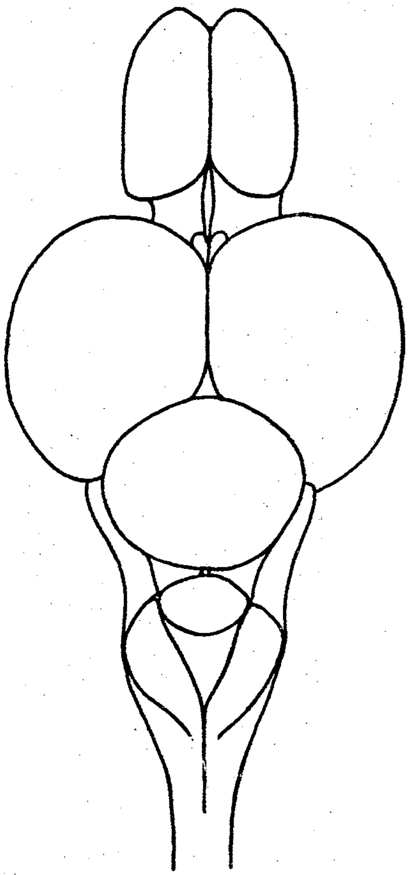

Fig. 18. Brain Pattern in Hybopsis bellica

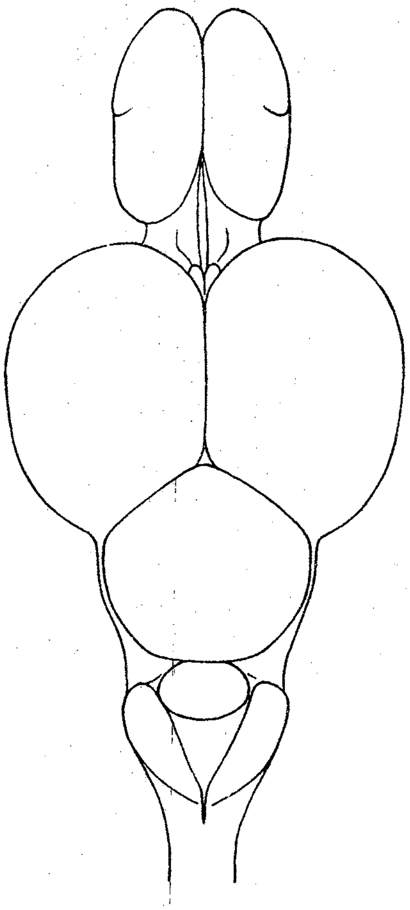

Fig. 19. Brain Pattern in Hybopsis biguttata

at the midline and are nearly identical in all species. The longitudinal torus is not visible externally because it is covered by the optic tectum. In Nocomis and other sight-feeding fishes of the genus Hybopsis the tori are cylindrical and united by a membrane along their entire length. The valvula is not developed to the same extent as in some Extrarius. The cerebellum is equal to or smaller than a single optic lobe in all Nocomis. In H. (Nocomis) sp. (Fig. 15) and H. micropogon (Fig. 16), the cerebellum projects posteriad over the anterior part of the facial lobe. In other species the cerebellum does not project as far posteriad. The hindbrain was similar in all species, except for the larger facial lobe in *H. leptocephala* (Fig. 17). Moderately developed vagal lobes are almost identical in all species with only slight differences in configuration.

Discussion: Species of *Nocomis* inhabit relatively clear waters, and have fewer taste buds (Table VI) than *Extrarius* from silty water (Table V). For example, *H. leptocephala* inhabits the Roanoke River of

TABLE VI

MEAN EXTERNAL AND INTERNAL TASTE BUDS PER SECTION FROM FIVE REGIONS IN *HYBOPSIS*, SUBGENUS *NOCOMIS*

Region*		*H. leptocephala*	H. (*Nocomis*) Sp.	*H. micropogon*	*H. biguttata*	*H. bellica*
1	A	42.0	33.4	30.2	30.0	27.6
	B	0.0	0.0	0.0	0.1	0.0
2	A	52.5	30.6	16.0	18.3	28.6
	B	9.8	8.7	5.6	8.1	4.1
3	A	24.4	11.2	11.3	9.2	12.5
	B	17.7	10.5	7.7	5.9	9.4
4	A	11.8	6.2	7.8	7.1	12.2
	B	28.5	25.2	28.1	20.3	18.6
5	A	11.7	5.6	8.1	5.7	11.2
	B	57.4	36.6	42.2	39.6	36.6

*1 = tip of snout, 2 = anterior of nasal rosette including the lips, 3 = posterior of nasal rosette, 4 = posterior of retina, 5 = anterior of cerebellum, A = number of external taste buds, B = number of internal taste buds

Virginia with a turbidity range of 0 to 75 Jackson units, whereas *H. a. tetranemus* inhabits the Arkansas River with a Jackson unit range of 25 to 5000 (U. S. Dept. of Health, Education and Welfare, 1962). Lachner (1950) reporting on the food habits of *H. micropogon* and *H. biguttata*, revealed that, by volume, 50 per cent of the adult diet was filamentous algae and vascular plants, with the remainder being animal material, primarily insects. He suggested that the plant material was probably taken accidentally with animal material. However, Fleming's (1959) study on *H. leptocephala* indicated that plant material (filamentous algae, diatoms and desmids) formed the bulk of food material throughout the year. He suggested that plant material was specifically selected. The intestines of most *Nocomis* are short, but in *H. leptocephala* and *H. bellica* they are longer and loop across the stomach (Moore, 1957). A longer intestine usually reflects ingestion and utilization of larger quantities of plant material.

All *Nocomis* are reasonably well supplied with cutaneous taste buds on the snout (Table VI). Taste-bud numbers decline rapidly posteriad from the tip of the snout except in *H. leptocephala* and *H. bellica*, which are apparently more reliant on cutaneous taste buds than are the other species of *Nocomis*. The numerous taste buds on the lips of *H. leptocephala* are primarily responsible for the increased size of the facial lobe. The proliferation of taste buds on the lips and the longer intestine probably facilitate ingestion and utilization of more plant material, especially by *H. leptocephala*.

Direct competition between closely related sympatric species may be reduced by development of slightly different food preferences or feeding behaviors. Such a change seems to have occurred between *H. micropogon* and *H. leptocephala*. However, *H. micropogon* and *H. biguttata* are also sympatric in part of their ranges, and from available data on food habits, brain patterns and gustatory components, they appear to be in direct competition. Lachner (1950, 1952) indicated some differences in habitat preference in both juveniles and adults, which may be the buffer that eases competition. Basic similarities in brain patterns reflect a uniformity of habitat selection and feeding behavior.

Internal taste-bud numbers are approximately the same in all species (Table VI). Density of internal taste buds increases posteriad (Table VI) but does not reach that attained in some *Extrarius* (Table V). Histological characteristics of the buccal cavity lining are uniform in *Nocomis*. The roof of the buccal cavity has numerous longitudinal folds with a thick epidermal layer, a heavy muscularis mucosa and scattered muscle bundles which increase in number posteriad. The greater abundance and size of the buccal folds suggests that these fishes are superior to *Extrarius* in selecting and sorting food items in the anterior buccal cavity.

Hybopsis biguttata was used as an example of a sight-feeding fish in behavioral observations. It was a restless fish, moving incessantly about the aquarium, two or three inches above the sand. Introduction of *Daphnia* sp. or dry food elicited an instant response; from its position near the bottom of the aquarium, it would often break water to secure food items. Preference for *Daphnia* sp. over dry food was shown with simultaneous introduction. Movement of the live food probably accounts for discrimination between these items by visual means.

Occasionally materials were picked up from the sand, but only when food was unavailable elsewhere. Often all or part of this material was immediately rejected, indicating gustatory and/or tactile discrimination on the lips or anterior buccal lining.

Subgenus *Hybopsis*

The subgenus *Hybopsis* contains five nominal species: *H. amblops*, *H. hypsinota*, *H. labrosa*, *H. rubrifrons* and *H. storeriana*.

Morphology: Members of this subgenus show no particular structural modification for a specific habitat-type. The body is more compressed than in *Nocomis*, with pectoral fins of approximately the same relative size. Eyes are large, snouts rather blunt and barbels small, in all except *H. labrosa*, with small eyes and well-developed barbels. Barbels are small with few taste buds in all except *H. labrosa* and are completely absent in some populations of *H. amblops* and *H. hypsinota* (Moore, 1957). This suggests that barbels are of limited use in feeding.

Brain pattern: Forebrain lobes vary considerably. In *H. amblops* (Fig. 20) and *H. rubrifrons* (Fig. 21) they are elongate, whereas in *H. hypsinota* (Fig. 22), *H. storeriana* (Fig. 23) and *H. labrosa* (Fig. 24) they are shorter. *H. storeriana* and *H. hypsinota* also exhibit dorsal enlargements. In *H. storeriana* and *H. labrosa*, forebrain lobes are nearer to the optic lobes than in other species. Optic lobes in this group are large and uniform in size and configuration, except in *H. labrosa*, where they are slightly smaller. The longitudinal torus is more cylindrical and less exposed in *H. amblops* and *H. rubrifrons* than

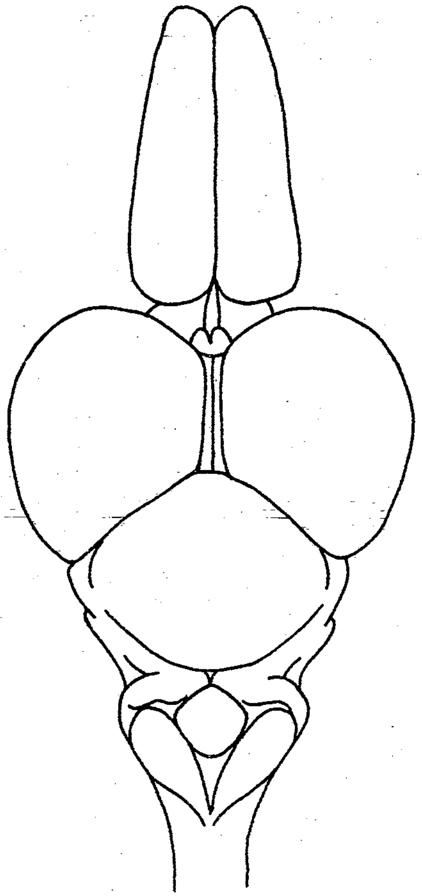

Fig. 20. Brain Pattern in *Hybopsis amblops*

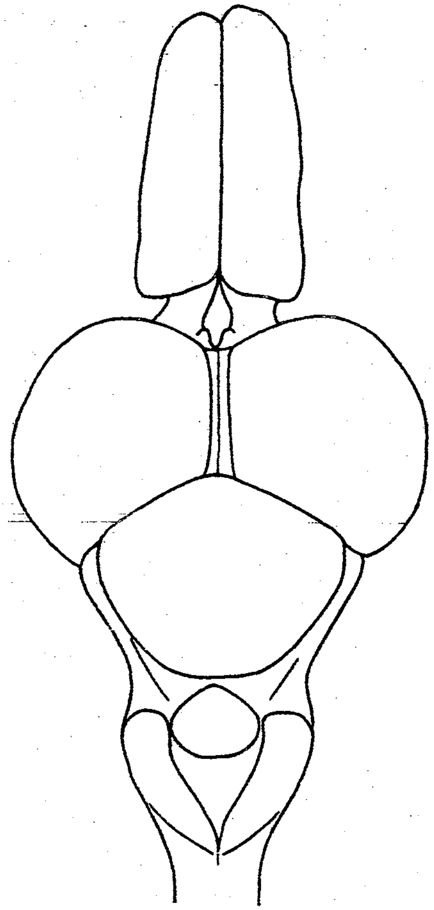

Fig. 21. Brain Pattern in *Hybopsis rubrifrons*

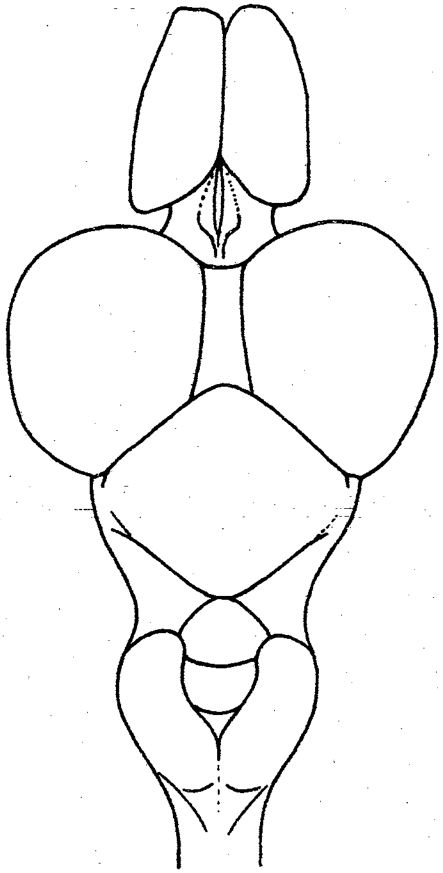

Fig. 22. Brain Pattern in Hybopsis hypsinota

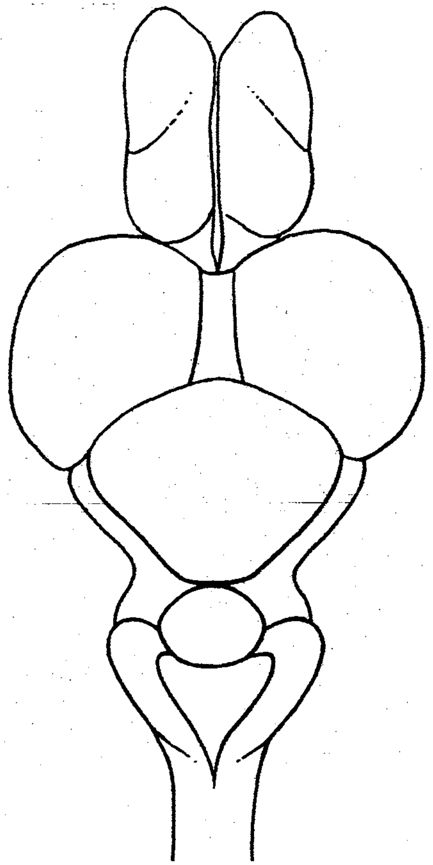

Fig. 23. Brain Pattern in Hybopsis storeriana

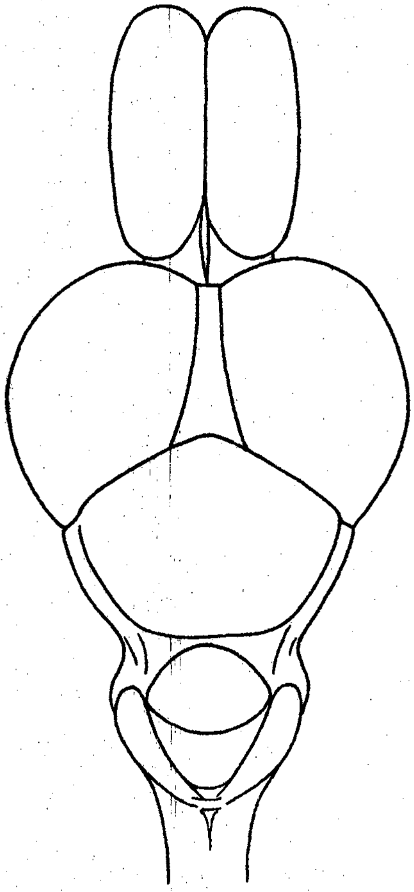

Fig. 24. Brain Pattern in *Hybopsis labrosa*

in the others. The cerebellum is similar in all species. Facial lobes are small in *H. amblops*, *H. rubrifrons* and *H. hypsinota* and slightly larger in *H. storeriana* and *H. labrosa* (Table III). Hyperdevelopment of the vagal lobes is superficially visible in *H. hypsinota* (Fig. 22), but is observable only in transverse section in *H. amblops*, *H. rubrifrons* and *H. storeriana*.

Discussion: The optic lobe/facial lobe width index can be used as an indication of relative size of the lobes and as a means for estimating relative density of cutaneous taste buds (Fig. 9). It can be seen that both H. storeriana and H. labrosa rely more on taste to secure food than do other species of the subgenus. External taste buds are slightly more numerous in H. storeriana and much more numerous in H. labrosa than in other species (Table VII). H. labrosa and H. storeriana also have well-developed compound taste buds in the interradial membranes of the pectoral fins. These are absent or reduced in other species (Table II). H. storeriana is known to inhabit streams of high turbidity in the Great Plains region. Trautman (1957) reported H. storeriana as an inhabitant of low or base-level streams in Ohio. If the water was clear, fish were found in deep pools, but when streams became turbid, they moved into riffle areas or higher-gradient streams. H. storeriana is often numerous in lakes. H. amblops is found in streams of moderate gradient and only rarely in high-gradient streams where sand and gravel cannot accumulate (Trautman, 1957). Moore and Paden (1950) collected H. storeriana in a turbid base-level stream, the Arkansas River, and H. amblops in a higher-gradient tributary, the Illinois River. H. amblops inhabits the Current River of Missouri where the turbidity ranges from one to four Jackson units (Missouri Water Pollution Board, 1963). It is significant that these two closely related species were in the same general area but exhibited different habitat preferences. According to the Ohio River investigations of Trautman (1957), H. storeriana is more tolerant of turbid waters than H. amblops, as evidenced by the rapid decline in population size of H. amblops as turbidity increased.

Methods of securing food in this group are probably variable. The most radical deviation is to be expected in H. labrosa, since it has the smallest eyes, longest barbels, largest facial lobe, greatest number of cutaneous taste buds and fewest internal taste buds. Consideration of the gustatory equipment possessed by this fish suggests that it could survive in more turbid environments than any other species of the subgenus except H. storeriana. Longitudinal folds in the anterior buccal cavity are numerous and deep, diminishing in number and size posteriad. This suggests that manipulation of food items may be best accomplished in the lip and pharyngeal region. However, density of taste buds in the pharyngeal region indicates that gustatory sensitivity is not well developed. Selection of food items is probably accomplished by an interaction of visual and external gustatory organs, leaving a minimum of sorting to be done in the pharyngeal region. It should be noted that histological data for H. labrosa were taken from a single specimen. More material is needed for a more definitive interpretation. External and internal taste-bud numbers are approximately equivalent in the remaining species, although H. amblops is practically devoid of external taste buds posteriad from the lip region (Table VII).

Inhabitants of turbid streams, such as H. storeriana, must rely more on cutaneous taste buds for detection of food, while species from clear water are able to rely primarily on visual detection. Clear-water inhabitants, such as H. amblops, usually have extremely low numbers of cutaneous taste buds (Table VII), reflecting a dependence on vision for securing food. Visual location of food items by H. hypsinota and H. rubrifrons is possibly enhanced by sensitive lips as shown by the increased number of taste buds in that region (Table VII).

It has previously been shown that H. amblops (and probably others in this group) avoid high-gradient streams where sand and detritus are flushed downstream. Regardless of the initial method of locating food, large quantities of detritus probably are ingested with the food items. Longitudinal folds in the lining of the anterior buccal cavity are numerous, of moderate size and often bifurcated. The folds diminish in size posteriad, but remain numerous through the pharyngeal region. Elaboration of the folds, coupled with enormous numbers of taste buds in the pharyngeal region (Table VII), give this group the most efficient sorting mechanism of all _Hybopsis_. Treatment of ingested food material is apparently the same in all except _H. labrosa_.

TABLE VII

MEAN EXTERNAL AND INTERNAL TASTE BUDS PER SECTION FROM FIVE REGIONS IN _HYBOPSIS_, SUBGENUS _HYBOPSIS_

Region*		_H. labrosa_	_H. storeriana_	_H. rubrifrons_	_H. amblops_	_H. hypsinota_
1	A	34.2	21.8	20.5	18.0	11.0
	B	0.0	0.0	0.0	0.0	0.0
2	A	32.8	30.9	43.0	22.2	45.8
	B	6.6	7.4	6.2	9.8	4.0
3	A	20.0	18.0	17.8	7.5	17.4
	B	5.5	15.6	15.7	11.1	15.8
4	A	14.9	7.2	6.2	2.5	12.2
	B	16.2	88.8	65.9	64.0	101.2
5	A	12.0	7.0	5.6	2.2	9.6
	B	30.5	138.2	157.9	125.1	120.0

*1 = tip of snout, 2 = anterior of nasal rosette including the lips, 3 = posterior of nasal rosette, 4 = posterior of retina, 5 = anterior of cerebellum, A = number of external taste buds, B = number of internal taste buds

H. storeriana was used for behavioral observations in the subgenus *Hybopsis*. It was easily excited by vibrations or movement near the aquarium. Feeding occurred only at or near the bottom. When not feeding, the fish rested quietly near a bottom corner of the aquarium. Discrimination of food items appeared to be under both visual and gustatory control. Capture of live or dry food seldom involved movement of more than one or two inches. Touching of the fish by either type of food elicited an apparent feeding response, but if the initial movement was unsuccessful, there were no subsequent attempts for that food item. If given a choice between live and dry food, a slight preference for live food was shown. Often, when there was dry food on the bottom, fish would pick up material, appear to chew it momentarily and eject large quantities of sand.

Subgenus *Erimystax*

Erimystax contains six nominal species, five of which were observed in the present study: *Hybopsis cahni*, *H. dissimilis*, *H. harperi*, *H. insignis* and *H. x-punctata*.

Morphology: Except for *H. harperi*, these fishes appear to be bottom dwellers inhabiting fast-flowing streams. Most species have terete, slightly compressed bodies, moderately-elongate pectoral fins, upward projecting eyes and inferior or subterminal mouths. In *H. harperi*, the body is more compressed, the mouth is terminal and oblique and the eyes are lateral. Barbels are conspicuous, flattened, elaborate structures, except in *H. harperi*, where they are inconspicuous or absent. In general, taste buds in *Erimystax* are larger than those in fishes of comparable size in other subgenera (Table I). Taste buds on the barbels of H. x-punctata are extremely large, sometimes attaining a length of 100 microns, and project downward at oblique angles to give the barbels a branched appearance. While the taste buds are large, there are generally fewer than 10 on a barbel. This casts doubts on the gustatory efficacy of barbels in this species.

Brain pattern: Forebrain lobes are basically similar in all Erimystax, broad posteriad and attenuated anteriad (Figs. 25-29). Optic lobes are well developed in all species, and the longitudinal torus is visible in H. cahni (Fig. 27), H. insignis (Fig. 25) and H. x-punctata (Fig. 26). The valvula shows no appreciable hyperdevelopment. The cerebellum extends posteriad over the anterior end of the facial lobes, except in H. harperi (Fig. 29). The cerebella in H. x-punctata and H. harperi are smaller than in other species of Erimystax. The facial lobe shows a marked increase in size in the following direction: H. harperi, H. cahni, H. dissimilis, H. x-punctata and H. insignis. There are no appreciable differences in size or configuration of the vagal lobes.

Discussion: Erimystax usually inhabits high-gradient streams with numerous riffles. Differences in cerebellum size correlate well with microhabitat differences. For example, the riffle-inhabiting H. x-punctata has a markedly smaller cerebellum than do other riffle-inhabiting Erimystax. Trautman (1957) pointed out that H. x-punctata was found in riffles while H. dissimilis was found at the base of the riffles. Moore and Paden (1950) went further in pinpointing the specific microhabitat of H. x-punctata beneath rocks in the riffle, where the effects of swift water would be reduced.

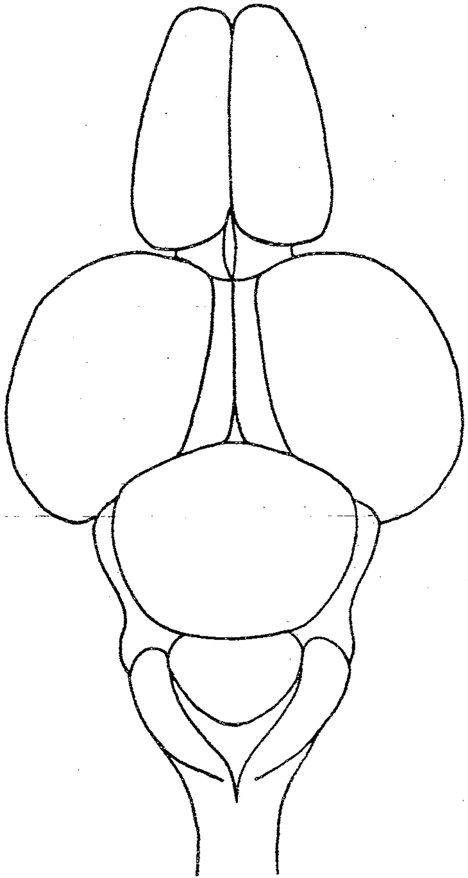

Fig. 25. Brain Pattern in *Hybopsis insignis*

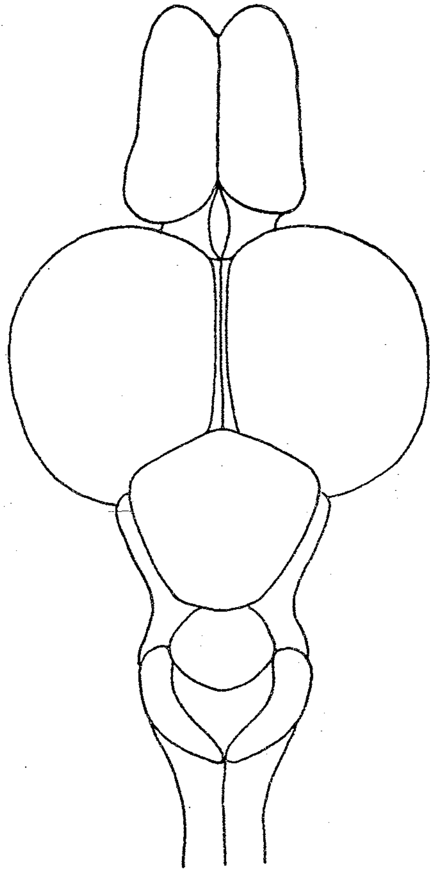

Fig. 26. Brain Pattern in *Hybopsis x-punctata*

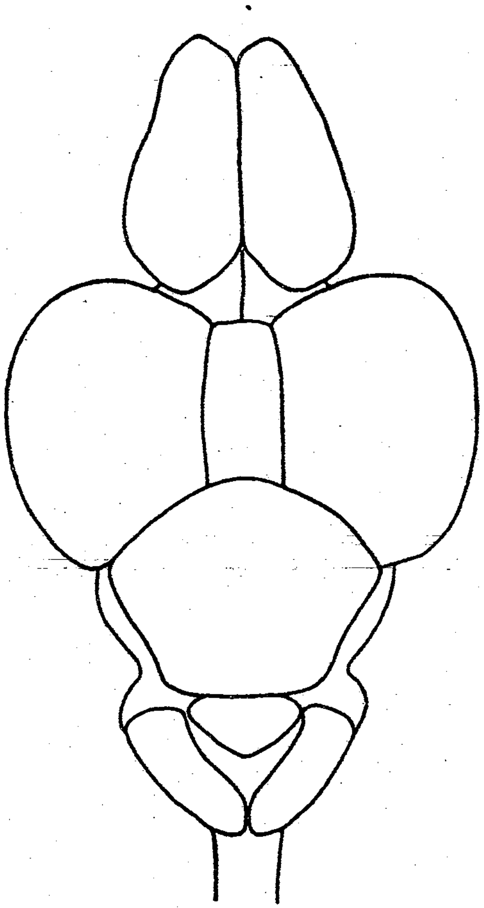

Fig. 27. Brain Pattern in *Hybopsis cahni*

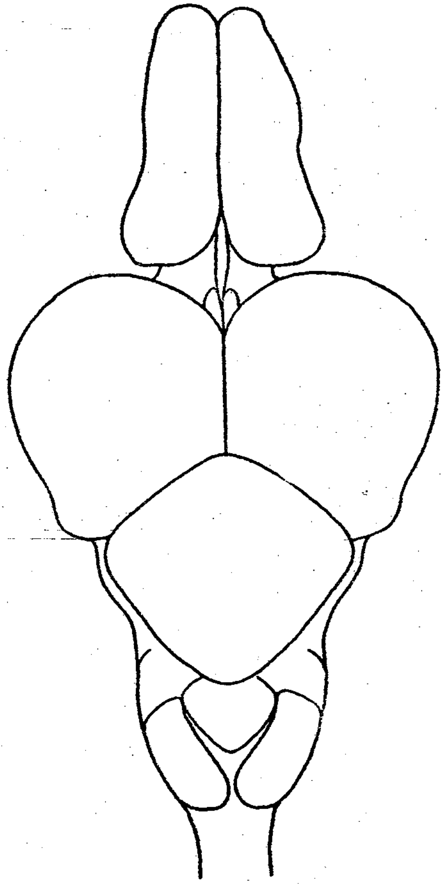

Fig. 28. Brain Pattern in *Hybopsis dissimilis*

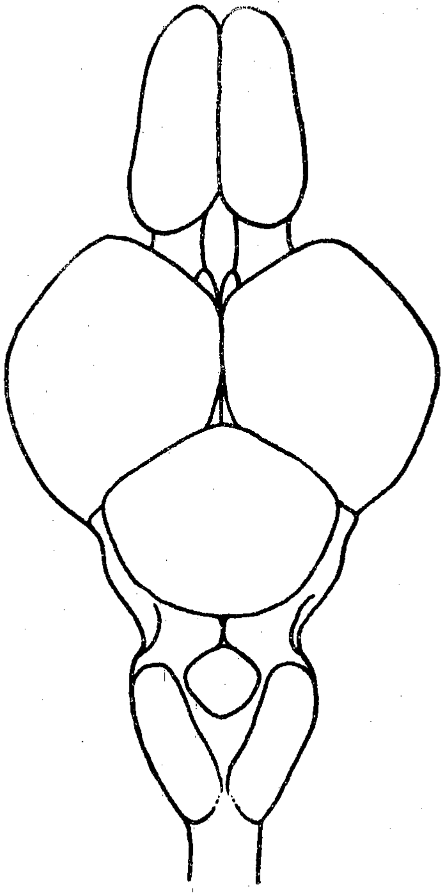

Fig. 29. Brain Pattern in *Hybopsis harperi*

Moore (1950) considered *H. x-punctata* as a silty-water species and *H. dissimilis* as a clear-water species. Trautman (1957) showed that both forms could occur in the same stream where habitat conditions were favorable. He stated that he "... frequently observed both forms feeding within a few inches of each other." Recent collections from the Powell River in Tennessee show that *H. dissimilis* is also sympatric with *H. cahni* and *H. insignis*. Competition among sympatric species could be reduced by different food requirements or different feeding behaviors. Although the food habits of these fishes are unknown, it is evident that different feeding mechanisms are in operation. External taste bud density is greater in H. x-punctata than in other species, especially on the tip of the snout and lips (Table VIII). In H. insignis, increased taste bud density occurs in the lip region. The enlarged, fleshy, subterminal lips probably contain a greater total number of taste buds than are found in any other species of Erimystax. Cutaneous taste bud proliferation is reflected in the increased size of the facial lobe in H. x-punctata and H. insignis (Figs. 25-26). In H. x-punctata, feeding is probably accomplished by probing under rocks and in crevices with its sensitive snout, while H. insignis uses its lips for food detection or discrimination. On the basis of cutaneous taste buds (Table VII) and brain morphology, it appears that H. dissimilis (Fig. 28), H. harperi (Fig. 29) and H. cahni (Fig. 27) locate food primarily by sight, enhanced by use of cutaneous taste buds.

Longitudinal folds in the lining of the anterior buccal cavity are numerous and highly convoluted in H. harperi and H. x-punctata, numerous, simple deep structures in H. dissimilis, numerous and low in H. insignis and few and deep in H. cahni. The folds diminish in size posteriad through the pharyngeal region where all species have numerous low folds. Erimystax has fewer internal taste buds than subgenera previously discussed, which may indicate that mechanisms for food location and ingestion are comparatively efficient (Table I).

Erimystax is basically a clear-water group, inhabiting areas with little detrital material on the bottom. Turbidity levels are usually low, as shown in the Nolichucky River (one to 32 Jackson units) inhabited by H. insignis. H. x-punctata was considered by Moore (1950) as a silty-water fish in Oklahoma, but Trautman (1957) indicated that both _H. x-punctata_ and _H. dissimilis_ are apparently intolerant of silty conditions in Ohio streams, as evidenced by their rapid decline with increased siltation.

TABLE VIII

MEAN EXTERNAL AND INTERNAL TASTE BUDS PER SECTION FROM FIVE REGIONS IN _HYBOPSIS_, SUBGENUS _ERIMYSTAX_

Region*		_H. x-punctata_	_H. harperi_	_H. dissimilis_	_H. insignis_	_H. cahni_
1	A	31.5	18.8	14.7	14.1	13.3
	B	0.2	0.0	0.0	0.0	0.0
2	A	33.3	16.5	17.0	29.6	9.6
	B	6.2	8.4	2.4	3.3	4.7
3	A	14.6	5.5	7.0	12.7	6.5
	B	5.5	7.2	4.2	5.4	3.8
4	A	7.7	4.0	6.9	5.8	5.0
	B	11.7	15.8	13.6	23.7	20.6
5	A	5.3	3.9	4.9	5.7	1.5
	B	34.6	29.5	22.2	27.9	20.0

*1 = tip of snout, 2 = anterior of nasal rosette including the lips, 3 = posterior of nasal rosette, 4 = posterior of retina, 5 = anterior of cerebellum, A = number of external taste buds, B = number of internal taste buds

Subgenus _Macrhybopsis_

This subgenus contain two nominal species: _Hybopsis gelida_ and _H. meeki_.

Morphology: Numerous morphological differences between these species indicate somewhat different habitat preferences or perhaps a more distant phylogenetic relationship than indicated by their current taxonomic positions. Both species inhabit extremely turbid streams and are often collected in the same locality. *H. meeki* has long falcate pectoral fins, very small eyes, sometimes covered with an overgrowth of skin, small barbels and a moderately compressed body. *H. gelida* has broad expensive pectoral fins, larger eyes, a subterminal mouth, conspicuous barbels and a less compressed body. Bailey and Allum (1962) reported that both species are found in strong currents, with *H. gelida* usually over gravel bottoms and *H. meeki* over sand bottoms.

Brain pattern: Brain patterns of *H. meeki* (Fig. 30) and *H. gelida* (Fig. 31) are the most aberrant of any *Hybopsis*, approached only by turbid-water forms of *Extrarius*. Forebrain lobes of *H. gelida* are larger and further from the optic lobes than in *H. meeki*. Both species have widely separated optic lobes which are extremely reduced. Optic lobes in *H. meeki* appear to be slightly larger than in *H. gelida*, although *H. gelida* has larger eyes. In both, the longitudinal tori are flattened into thin sheets of tissue (Fig. 6), connected by a membrane anteriad and separated widely posteriad. The valvula shows extreme hyperdevelopment, projecting well forward into the third ventricle. It appears that the valvula fills the posterior part of the ventricle and exerts an outward pressure, forcing the optic lobes apart and applying tension on the tori. The tori are eventually separated posteriad, allowing the valvula to be exposed. The cerebellum in *Macrhybopsis* is well developed, especially in *H. gelida*. The relative

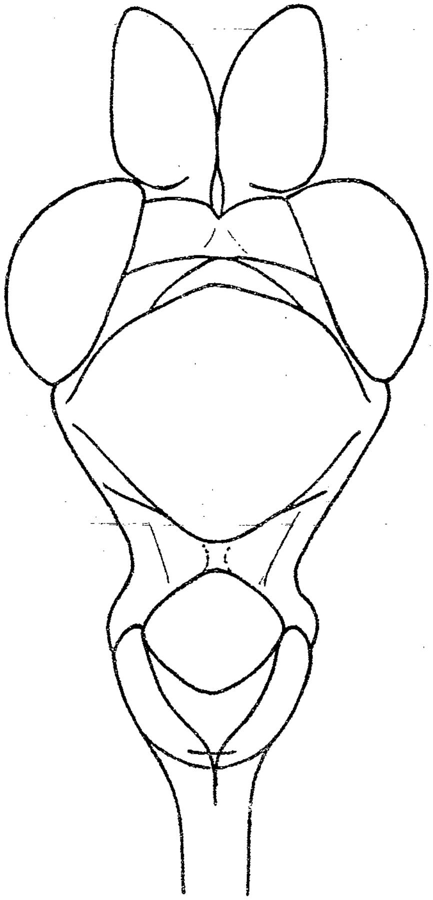

Fig. 30. Brain Pattern in *Hybopsis meeki*

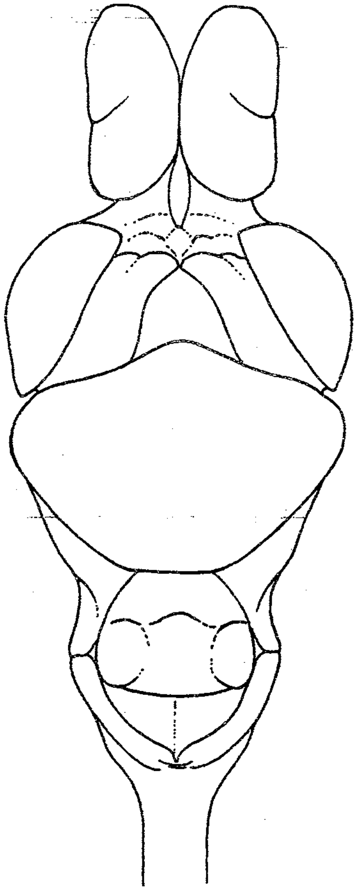

Fig. 31. Brain Pattern in *Hybopsis gelida*

size of the cerebellum tends to indicate residence in swift waters. Facial lobes are well developed in both species, though differences in configuration are quite noticeable. In H. gelida, the facial lobe is expanded laterally, with dorsal swellings on the extremities, while in H. meeki, the facial is more spherical as in Extrarius. The vagal lobes are similar in the two species, but slightly larger in H. meeki.

Discussion: Macrhybopsis inhabits large rivers with constant high turbidity; 120 to 1840 (mean 363.9) Jackson units in the Mississippi River at Cape Girardeau, Missouri (U. S. Dept. of Health, Education and Welfare, 1962). Since these are basically bottom-dwelling fishes, available light is, at best, very limited. Residence in this darkened habitat has resulted in reduced eye and optic lobe size with a compensatory increase in cutaneous taste buds (Table IX). Density of cutaneous taste buds in H. gelida is relatively constant for the areas observed while in H. meeki it declines posteriad from the lip region. Internal taste buds are abundant in the pharyngeal region in H. meeki but reach only modest numbers in H. gelida (Table IX). Arrangement of the longitudinal folds in the lining of the buccal and pharyngeal cavities of these species is different, particularly in the pharyngeal region. Both differ from other species of the genus Hybopsis in that the anterior buccal folds are low and widely separated, suggesting that manipulation of food material would be difficult. In the pharyngeal region, H. meeki has numerous low folds which contain abundant taste buds, while H. gelida has no folds and far fewer taste buds.

According to Moore (1950), Macrhybopsis "... probably possess the most highly developed cutaneous sense organs of any of the North American cyprinids." This certainly appears to be true in H. gelida;

however, *H. meeki* is surpassed in this respect by turbid-water *Extrarius*. *H. gelida* appears to be better adapted than *H. meeki* for survival in its preferred habitat, since it has more cutaneous taste buds and larger eyes. Relative abundance of the two species as reported by Bailey and Allum (1962) indicate that each has some unique adaptive specialization. *H. gelida* is less common in the Mississippi River below Kansas City, Missouri. Both species are common in the middle parts of the Missouri River, but only *H. gelida* occurs in the upper Missouri River system.

TABLE IX

MEAN EXTERNAL AND INTERNAL TASTE BUDS PER SECTION FROM FIVE REGIONS IN *HYBOPSIS*, SUBGENUS *MACRHYBOPSIS*

Region*		*H. meeki*	*H. gelida*
1	A	33.1	56.1
	B	0.0	0.0
2	A	36.6	53.1
	B	7.5	6.2
3	A	19.9	56.1
	B	12.8	8.9
4	A	14.6	52.8
	B	41.4	22.3
5	A	10.6	47.4
	B	64.4	36.1

*1 = tip of snout, 2 = anterior of nasal rosette including the lips, 3 = posterior of nasal rosette, 4 = posterior of retina, 5 = anterior of cerebellum, A = number of external taste buds, B = number of internal taste buds

There probably are two slightly different feeding mechanisms in operation in these two species. Awareness of food in the immediate environment must be more acute in *H. gelida*, due to the extreme density of cutaneous taste buds. Longer barbels and numerous ridges or papillae on the chin and isthmus region provide more surface area for taste buds in *H. gelida*. Sorting and concentration of food material in the pharyngeal cavity are apparently more efficient in *H. meeki* because of numerous longitudinal folds and generous distribution of internal taste buds. It is possible that different feeding mechanisms tend to balance species numbers where habitat is available for both. *H. gelida* may detect food more readily than *H. meeki* but must be more selective initially, since it has a less efficient internal sorting mechanism. *H. meeki*, however, may be able to ingest quantities of detritus with the food by virtue of a more efficient internal sorting mechanism. The possible difference in feeding mechanisms may explain *H. meeki's* preference for sand bottoms and *H. gelida's* for gravel bottoms.

Subgenus *Platygobio*

This subgenus contains a single nominal species, *Hybopsis gracilis*, with two nominal subspecies, *H. g. gracilis* and *H. g. gulonella* (Olund and Cross, 1961). In the present study no distinction was made between the two subspecies.

Morphology: As indicated by the name, flathead chub, *H. gracilis* is characterized by a depressed head. It has a slightly compressed body, moderately large falcate pectoral fins, a large subterminal mouth and well-developed barbels.

Brain pattern: Forebrain lobes in *H. gracilis* (Fig. 32) are extremely short, laterally expanded structures. While the forebrain lobes are quite different from those in most other species, it is doubtful that any functional significance can be attributed to their shape. Rather, the short, depressed snout probably has the greater influence on forebrain shape. Optic lobes are moderately reduced, with a slight separation at the midline. Longitudinal tori are visible posteriad and concealed anteriad by the optic lobes. Development of the valvula and cerebellum is moderate. In the hindbrain, both facial and vagal lobes are well developed.

Discussion: According to Bailey and Allum (1962), *H. gracilis* is often the dominant minnow in streams of high turbidity. Olund and Cross (1961) defined the habitat as turbid streams of moderate current with sandy bottoms or murky pools with gravel or bedrock, depending on the subspecies. They observed *H. gracilis* in the Purgatoire River congregated one to four inches above the bottom, near or under roots and debris. They also noted that the fish occasionally rose to the surface and theorized that the fish were feeding.

As in other *Hybopsis* with reduced optic lobes, there are large numbers of cutaneous taste buds (Table X). Internal taste buds are also fairly numerous in the pharyngeal region. Numerous compound taste buds are found in the first interradial membrane of the pectoral fins. Moore (1950) found more of these compound taste buds in the silty-water subspecies *H. g. gracilis* (*H. g. communis* of Moore) than in *H. g. gulonella* inhabiting clearer waters.

TABLE X

MEAN EXTERNAL AND INTERNAL TASTE BUDS PER SECTION FROM FIVE REGIONS IN <u>HYBOPSIS</u> <u>GRACILIS</u>, SUBGENUS <u>PLATYGOBIO</u>

Region*									
1		2		3		4		5	
A	B	A	B	A	B	A	B	A	B
40.9	1.2	31.8	13.3	26.1	12.3	15.4	24.3	18.4	53.6

*1 = tip of snout, 2 = anterior of nasal rosette including the lips, 3 = posterior of nasal rosette, 4 = posterior of retina, 5 = anterior of cerebellum, A = number of external taste buds, B = number of internal taste buds

Success of this species appears dependent on its ability to take advantage of changing environmental conditions. No single sensory mechanism is extremely well developed. Conversely, no single sensory system has degenerated to a point where its utility is seriously impaired. From data presented by Olund and Cross (1961), it appears that <u>H. gracilis</u> is a fortuitous feeder. They showed that food was primarily terrestrial insects, with plants prominent in some areas. In one area, 99 per cent of the food volume was algae. One could assume that adult insects, whether terrestrial or aquatic, are taken visually from the water surface. Even in extremely turbid waters, light rays penetrate the first few inches and could provide sufficient light for sight feeding. Abundant taste buds on the snout, barbels, lips and pectoral fins evidently allow adequate chemical sensitivity to detect and secure food items without resorting to visual means. The ability to utilize both means of securing food places <u>H. gracilis</u> at a selective advantage over fishes which must rely on a single method, particularly in an environment varying between clear and extremely turbid conditions.

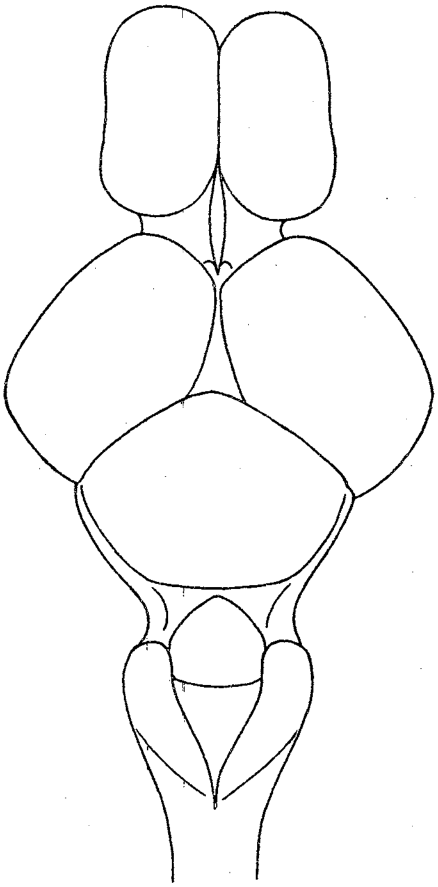

Fig. 32. Brain Pattern in Hybopsis gracilis

Few anterior buccal longitudinal folds occur, but they increase in height and number posteriad. In the pharyngeal region, the folds are again reduced in size and number but internal taste buds become abundant. This arrangement of folds and taste buds should provide a reasonably efficient internal sorting mechanism.

Subgenus Couesius

Morphology: The single nominal species, Hybopsis plumbea, is unique among Hybopsis in that the barbel is located forward from the posterior end of the maxilla. Small scales, small rounded pectoral fins, lateral moderately-large eyes, a short, depressed snout, slightly compressed body and an oblique terminal mouth characterize H. plumbea. Simon (1946) identified H. plumbea with cold-water lakes and streams, and indicated that it preferred small creeks to larger streams. He further stated that it was particularly abundant in thickly-weeded irrigation canals in parts of Wyoming. H. plumbea and H. gracilis are sometimes taken from the same stream. Usually H. plumbea is in the clear headwaters and H. gracilis in more turbid downstream areas (Personius and Eddy, 1955).

Brain pattern: Forebrain lobes are rectangular with dorsal swellings anteriad. They are closely adjoined to the well-developed optic lobes. A peculiar indentation in the posterior part of each optic lobe was noted in small specimens of other species, but was relatively constant in H. plumbea of all sizes. Separation of the optic lobes at the midline and exposure of the longitudinal tori is similar to that seen in H. gracilis. The cerebellum is well developed, less so in lake than in stream specimens. Facial and vagal lobes are moderately developed (Fig. 33).

Discussion: In view of the density of cutaneous and internal taste buds, H. plumbea must be considered as almost an obligatory sight feeder (Table XI). Paucity of external taste buds practically precludes their function as an essential part of the feeding mechanism. Figure 9

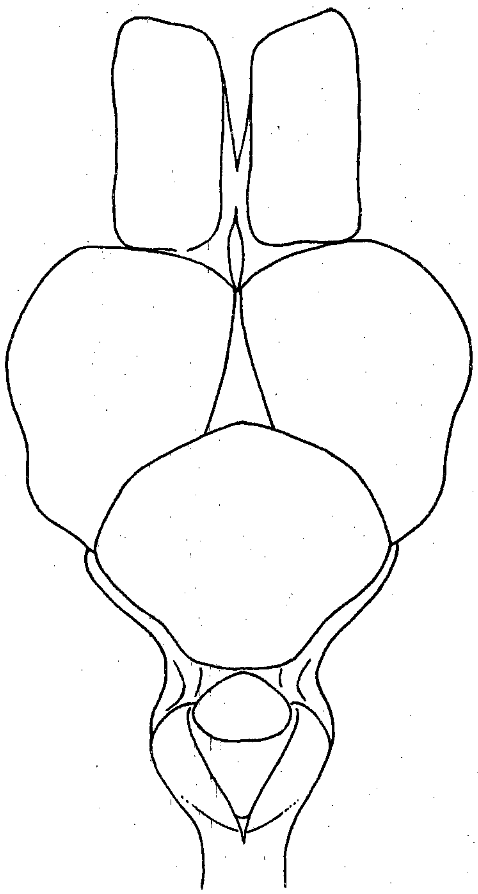

Fig. 33. Brain Pattern in Hybopsis plumbea

shows that H. plumbea uses vision probably to a greater extent than cutaneous taste buds. Simon (1946) indicated that H. plumbea was carnivorous, feeding primarily on insect larvae. The longitudinal buccal folds are numerous and deep with a heavy epidermal layer, but become smaller and less numerous in the pharyngeal region. An extremely low number of internal taste buds probably does not permit efficient sorting and concentration of food items.

TABLE XI

MEAN EXTERNAL AND INTERNAL TASTE BUDS PER SECTION FROM FIVE REGIONS IN HYBOPSIS PLUMBEA, SUBGENUS COUESIUS

Region*									
1		2		3		4		5	
A	B	A	B	A	B	A	B	A	B
12.5	1.4	10.3	5.2	5.4	4.6	4.3	10.3	3.9	22.1

*1 = tip of snout, 2 = anterior of nasal rosette including the lips, 3 = posterior of nasal rosette, 4 = posterior of retina, 5 = anterior of cerebellum, A = number of external taste buds, B = number of internal taste buds

Subgenus Oregonichthys

Morphology: The single nominal species, Hybopsis crameri, has characteristics that indicate a habitat in clear, slowly moving or standing waters, possibly with abundant vegetation. It has an extremely compressed body, short snout, large eyes and a terminal oblique mouth with a reduced barbel at the posterior end of the maxilla. Turbidity values for the Williamette River, inhabited by H. crameri, range from 3 to 26 (mean 11.5) Jackson units (Oregon State Board of Health, 1965).

Brain pattern: As in other short-snouted Hybopsis, the forebrain lobes (Fig. 34) are shortened, expanded laterad and closely adjoined to the optic lobes. Table III shows that development of the optic lobes is relatively greater than in other Hybopsis. Longitudinal tori are concealed beneath the optic tectum (Fig. 5). The valvula and cerebellum are not well developed. In the hindbrain, the facial lobe is small while the vagal lobes appear to be well developed. However, cross-sectional views reveal comparatively poor development of the vagal lobes.

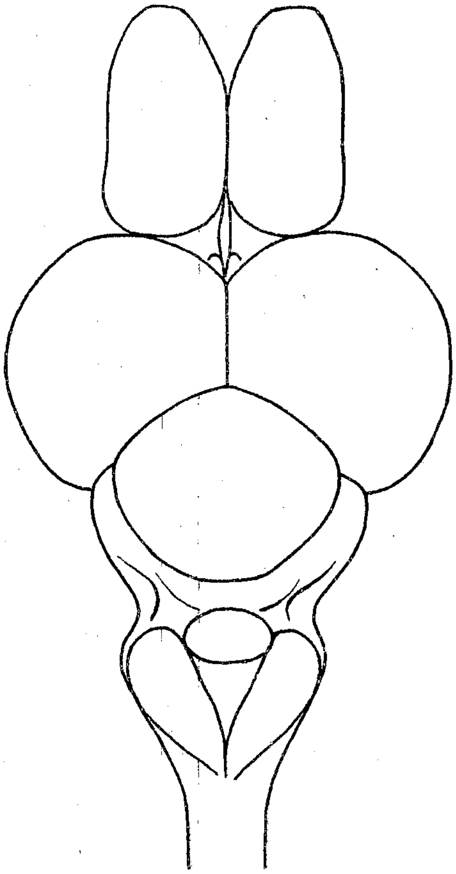

Fig. 34. Brain Pattern in Hybopsis crameri

Discussion: Abundance and distribution of external and internal taste buds are almost identical in this species and in H. plumbea (Table XII). Because of the paucity of cutaneous taste buds and the development of the optic lobes, H. crameri also must be considered as an obligatory sight feeder. Structure and development of the longitudinal folds and internal taste bud density are almost identical to those of H. plumbea.

TABLE XII

MEAN EXTERNAL AND INTERNAL TASTE BUDS PER SECTION FROM FIVE REGIONS IN HYBOPSIS CRAMERI, SUBGENUS OREGONICHTHYS

Region*									
1		2		3		4		5	
A	B	A	B	A	B	A	B	A	B
13.4	0.0	11.6	4.2	4.0	6.0	2.3	14.2	2.6	22.4

*1 = tip of snout, 2 = anterior of nasal rosette including the lips, 3 = posterior of nasal rosette, 4 = posterior of retina, 5 = anterior of cerebellum, A = number of external taste buds, B = number of internal taste buds

Statistical Analysis

Structural variablity in fishes may be attributed to mechanisms which are either genetically fixed or which are influenced by local environmental conditions. While structural differences are often apparent, it is difficult or impossible to isolate the specific mechanism responsible for these differences. Statistical analyses of brain lobes among <u>Hybopsis</u> species show many differences not apparent in visual observations. The analyses, however, show neither direction nor causal mechanism involved in the difference. Sometimes a functional basis for differences can be seen by comparing habitats, feeding habits and afferent sensory systems of species in question.

Analyses of 15 dependent variables (Fig. 1) adjusted for the independent variable (total brain length) were attempted among the species. Nine variables were adjudged to have homogeneous linear regression slopes and nonhomogeneous adjusted means among species. Heterogeneous linear regression slopes precluded testing of adjusted means, hence the omission of the remaining six variables from the analyses. Omission, however, does not indicate that differences do not exist. Small sample size often does not allow rejection of the null hypothesis of similarity when a larger sample size might indicate a significant difference. *Hybopsis cahni*, *H. labrosa* and *H. crameri* are included in the analyses on the basis of single specimens. Comparisons involving statistical analysis of these species should be viewed with reservation.

For each brain lobe analyzed, there were 210 comparisons among all species. Variability among species is greater for some lobes, as shown by the total number of significant differences: cerebellum width (77) and total optic width (76) (Table XIII), rhomboid fossa length (57) and rhomboid fossa width (70)(Table XIV), forebrain length (68) and forebrain width (94) (Table XV), optic length (94) and optic width (100) (Table XVI) and facial width (127) (Table XVII). The greatest number of differences occur in those lobes associated with a specific sensory function. Table XVII shows that similarity among species is often greatest within a subgenus or among those species with similar habitat requirements.

TABLE XIII

SIGNIFICANT DIFFERENCES IN TOTAL OPTIC WIDTH AND CEREBELLUM WIDTH IN HYBOPSIS

	H. leptocephala	H. (Nocomis) sp.	H. micropogon	H. biguttata	H. bellica	H. x-punctata	H. harperi	H. dissimilis	H. insignis	H. cahni	H. labrosa	H. storeriana	H. rubrifrons	H. amblops	H. hypsinota	H. gracilis	H. crameri	H. plumbea	H. meeki	H. gelida	H. aestivalis
H. leptocephala		-	-	-	+	-	+	-	-	-	-	-	+	+	-	-	-	-	-	+	+
H. (Nocomis) sp.	-		-	-	+	-	+	-	-	-	-	+	+	+	-	+	-	-	-	+	+
H. micropogon	-	-		-	-	-	+	+	+	-	-	-	+	+	-	-	-	-	-	+	+
H. biguttata	-	-	-		+	-	+	-	-	-	-	+	+	+	-	-	-	-	-	+	+
H. bellica	+	-	-	-		-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
H. x-punctata	-	-	-	-	-		+	-	-	-	-	-	-	+	-	-	-	-	-	+	+
H. harperi	+	+	-	+	-	-		+	+	+	-	+	-	-	+	+	-	+	-	-	-
H. dissimilis	-	-	-	-	-	-	+		-	-	-	+	+	+	+	+	-	+	+	+	+
H. insignis	-	-	+	-	+	-	+	-		-	+	+	+	+	+	+	-	+	+	+	+
H. cahni	-	-	-	-	-	-	-	-	-		-	-	+	+	-	-	-	-	-	+	+
H. labrosa	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-
H. storeriana	-	+	+	-	+	-	+	-	-	-	-		-	+	-	-	-	-	-	+	+
H. rubrifrons	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-
H. amblops	+	+	+	+	-	-	-	+	+	+	-	+	+		+	+	-	+	-	-	-
H. hypsinota	+	-	-	-	-	-	-	-	+	-	-	+	-	-		-	-	-	-	+	+
H. gracilis	+	+	+	+	+	+	+	+	-	-	-	+	+	+	+		-	-	-	+	+
H. crameri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
H. plumbea	-	+	+	+	+	+	+	+	-	-	-	-	+	+	+	-	-		-	+	+
H. meeki	-	+	+	+	+	+	+	+	-	-	-	-	+	+	+	-	-	-		-	-
H. gelida	+	+	+	+	+	+	+	+	+	-	-	+	+	+	+	-	-	-	-		-
H. aestivalis	-	-	-	-	+	-	+	-	-	-	-	-	-	+	+	+	-	+	+	+	

Total Optic Width

Cerebellum Width

+ indicates significance at the 1% confidence level

TABLE XIV

SIGNIFICANT DIFFERENCES IN RHOMBOID FOSSA LENGTH AND WIDTH IN HYBOPSIS

	H. leptocephala	H. (Nocomis) sp.	H. micropogon	H. biguttata	H. bellica	H. x-punctata	H. harperi	H. dissimilis	H. insignis	H. cahni	H. labrosa	H. storeriana	H. rubrifrons	H. amblops	H. hypsinota	H. gracilis	H. crameri	H. plumbea	H. meeki	H. gelida	H. aestivalis
H. leptocephala		-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	+	-
H. (Nocomis) sp.	-		-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	+	+
H. micropogon	-	-		-	+	+	-	+	+	-	-	+	-	-	-	+	-	-	+	+	+
H. biguttata	-	+	+		+	+	-	-	+	-	-	+	-	-	-	+	-	-	+	+	+
H. bellica	+	+	+	-		-	+	-	-	-	-	-	-	+	-	-	-	-	-	+	-
H. x-punctata	-	-	-	-	-		+	-	-	-	-	-	-	+	+	-	-	+	-	+	+
H. harperi	-	+	+	-	-	-		-	+	-	-	+	-	-	-	+	-	-	+	+	+
H. dissimilis	-	-	-	+	+	-	+		+	-	-	-	-	-	-	+	-	-	-	+	+
H. insignis	-	-	-	+	+	-	+	-		-	-	+	+	+	+	-	+	+	-	-	-
H. cahni	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-
H. labrosa	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-
H. storeriana	+	+	-	+	-	+	+	+	+	+	-		-	+	-	+	-	-	-	+	+
H. rubrifrons	+	+	-	-	-	-	-	+	+	-	-	+		-	-	+	-	-	-	+	+
H. amblops	+	+	+	-	-	-	-	+	+	-	-	+	-		-	+	-	-	+	+	+
H. hypsinota	-	+	+	-	-	-	-	+	+	-	-	+	-	-		+	-	-	+	+	+
H. gracilis	+	+	+	-	-	-	-	+	+	-	-	+	-	-	-		-	+	-	-	-
H. crameri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	+	-
H. plumbea	-	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-		+	+	+
H. meeki	-	+	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-		-	-
H. gelida	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-		+
H. aestivalis	-	+	+	-	-	-	-	-	+	-	-	+	-	+	-	+	-	-	-	-	

Rhomboid Fossa Width

Rhomboid Fossa Length

+ indicates significance at the 1% confidence level

TABLE XV

SIGNIFICANT DIFFERENCES IN FOREBRAIN LENGTH AND WIDTH IN HYBOPSIS

	H. leptocephala	H. (Nocomis) sp.	H. micropogon	H. biguttata	H. bellica	H. x-punctata	H. harperi	H. dissimilis	H. insignis	H. cahni	H. labrosa	H. storeriana	H. rubrifrons	H. amblops	H. hypsinota	H. gracilis	H. crameri	H. plumbea	H. meeki	H. gelida	H. aestivalis
H. leptocephala		+	+	-	-	-	-	+	+	-	-	-	+	+	-	-	-	-	-	-	-
H. (Nocomis) sp.	-		-	-	+	-	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-
H. micropogon	-	-		+	+	+	+	-	-	-	-	+	-	+	-	+	-	+	+	+	+
H. biguttata	+	-	-		+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-
H. bellica	-	-	-	-		+	-	+	+	+	+	-	+	+	+	+	-	-	-	-	+
H. x-punctata	+	+	+	-	-		-	-	+	-	-	-	-	-	-	+	-	-	-	+	-
H. harperi	+	+	+	-	-	-		+	+	-	-	-	+	+	-	-	-	-	-	-	+
H. dissimilis	+	+	+	+	-	-	-		-	-	-	-	-	-	-	+	-	+	-	+	-
H. insignis	+	+	+	-	-	-	-	-		-	-	-	-	-	-	+	-	+	+	+	+
H. cahni	-	-	-	-	-	-	-	-	-		-	-	-	-	-	+	-	-	-	+	-
H. labrosa	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-
H. storeriana	+	+	+	+	-	-	-	-	-	-	-		-	-	-	+	-	+	-	+	-
H. rubrifrons	+	+	+	+	+	+	+	+	+	+	+	+		-	-	+	-	+	-	+	-
H. amblops	+	+	+	+	+	+	+	+	+	+	+	+	-		-	+	-	+	-	+	-
H. hypsinota	+	+	+	+	-	-	-	-	-	-	-	-	+	-		+	-	+	-	+	-
H. gracilis	-	+	+	+	+	-	+	+	+	-	-	+	+	+	+		-	-	-	-	+
H. crameri	-	-	-	+	+	+	+	+	+	-	-	+	+	+	+	-		-	-	-	-
H. plumbea	-	-	-	-	-	+	+	+	+	-	-	+	+	+	+	+	-		-	-	+
H. meeki	-	-	-	-	-	-	-	+	-	-	-	+	+	+	+	-	-	-		-	-
H. gelida	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-	-	-		+
H. aestivalis	+	+	+	-	-	-	-	-	-	-	-	+	+	+	-	+	+	+	-	-	

Forebrain Width

Forebrain Length

+ indicates significance at the 1% confidence level

TABLE XVI

SIGNIFICANT DIFFERENCES IN OPTIC LOBE LENGTH AND WIDTH IN HYBOPSIS

	H. leptocephala	H. (Nocomis) sp.	H. micropogon	H. biguttata	H. bellica	H. x-punctata	H. harperi	H. dissimilis	H. insignis	H. cahni	H. labrosa	H. storeriana	H. rubrifrons	H. amblops	H. hypsinota	H. gracilis	H. crameri	H. plumbea	H. meeki	H. gelida	H. aestivalis
H. leptocephala		-	-	-	-	-	+	-	-	-	+	+	+	+	-	+	-	-	+	+	+
H. (Nocomis) sp.	-		-	-	-	-	+	-	-	-	+	+	+	+	-	+	-	-	+	+	+
H. micropogon	-	-		-	-	-	+	-	-	-	-	+	+	+	-	+	-	-	+	+	+
H. biguttata	-	-	-		-	-	+	-	-	-	+	+	+	+	-	+	-	-	+	+	+
H. bellica	-	-	-	-		-	-	-	-	-	-	-	+	+	-	+	-	-	+	+	+
H. x-punctata	-	-	-	-	-		-	-	-	-	-	-	+	+	-	+	-	-	+	+	+
H. harperi	+	+	+	+	-	+		+	+	-	-	-	-	-	-	-	-	+	+	+	+
H. dissimilis	-	-	+	-	+	+	+		-	-	-	+	+	+	-	+	-	-	+	+	+
H. insignis	-	-	-	-	-	-	+	-		-	-	-	+	+	-	+	-	-	+	+	+
H. cahni	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	+	-
H. labrosa	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	+	-
H. storeriana	+	+	+	+	+	+	-	+	+	-	-		-	-	+	-	-	+	+	+	+
H. rubrifrons	+	+	+	+	+	-	-	+	+	-	-	-		-	+	-	+	+	+	+	+
H. amblops	+	+	+	+	+	+	-	+	+	-	-	-	-		+	-	-	+	+	+	+
H. hypsinota	+	+	-	+	-	-	-	+	+	-	-	-	+	+		+	-	-	+	+	+
H. gracilis	+	+	+	+	+	+	-	+	+	-	-	-	-	-	-		+	+	+	+	+
H. crameri	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-		-	+	+	+
H. plumbea	-	-	-	-	-	-	+	+	-	-	-	+	+	+	-	+	-		+	+	+
H. meeki	+	-	-	+	+	+	-	+	+	-	-	-	-	-	-	-	-	+		-	-
H. gelida	+	+	+	+	+	+	+	+	+	+	+	-	-	-	+	+	+	+	-		+
H. aestivalis	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	-	-	

Optic Width

Optic Length

+ indicates significance at the 1% confidence level

TABLE XVII

SIGNIFICANT DIFFERENCES IN FACIAL LOBE WIDTH AND SPECIES SIMILARITY IN *HYBOPSIS*

	H. leptocephala	*H. (Nocomis) sp.*	*H. micropogon*	*H. biguttata*	*H. bellica*	*H. x-punctata*	*H. harperi*	*H. dissimilis*	*H. insignis*	*H. cahni*	*H. labrosa*	*H. storeriana*	*H. rubrifrons*	*H. amblops*	*H. hypsinota*	*H. gracilis*	*H. crameri*	*H. plumbea*	*H. meeki*	*H. gelida*	*H. aestivalis*
H. leptocephala		-	+	+	-	-	+	-	+	-	-	-	+	+	+	-	-	-	+	+	+
H. (Nocomis) sp.	8		-	+	-	+	+	-	+	-	-	-	+	+	+	+	-	-	+	+	+
H. micropogon	7	8		-	+	+	-	+	+	-	+	+	-	+	+	+	-	-	+	+	+
H. biguttata	7	7	7		+	+	-	+	+	-	+	+	-	+	-	+	-	+	+	+	+
H. bellica	6	6	5	5		-	+	-	+	-	-	-	+	+	+	-	-	-	+	+	+
H. x-punctata	6	7	5	2	8		+	-	+	-	-	-	+	+	+	-	-	+	-	+	-
H. harperi	3	1	3	5	7	5		+	+	-	+	+	-	+	-	+	-	+	+	+	+
H. dissimilis	7	7	4	6	5	8	2		+	-	-	-	+	+	+	+	-	-	+	+	+
H. insignis	5	6	4	5	4	7	1	7		+	-	+	+	+	+	+	+	+	-	+	-
H. cahni	9	9	9	9	8	9	8	9	8		-	-	-	+	+	-	-	-	-	+	-
H. labrosa	8	8	8	7	9	9	8	9	8	9		-	+	+	+	+	-	-	-	+	-
H. storeriana	5	4	1	2	6	7	4	4	4	8	9		-	+	+	+	-	-	+	+	+
H. rubrifrons	2	3	4	5	4	5	7	3	2	7	7	6		+	-	+	-	-	+	+	+
H. amblops	1	2	1	3	3	3	6	2	1	5	7	3	7		-	+	-	+	+	+	+
H. hypsinota	4	5	6	7	7	7	8	5	2	8	8	5	6	6		+	-	+	+	+	+
H. gracilis	4	0	1	2	5	4	4	0	2	8	9	3	4	3	3		+	+	-	+	-
H. crameri	9	9	9	8	8	8	8	8	6	9	9	8	6	7	8	7		-	+	+	+
H. plumbea	9	6	6	7	8	5	3	5	3	9	9	4	3	2	5	4	9		+	+	+
H. meeki	6	4	2	4	5	6	5	1	4	9	9	6	5	4	4	8	7	5		+	-
H. gelida	3	2	2	2	4	2	4	2	2	4	6	2	4	3	2	4	5	4	8		+
H. aestivalis	4	2	1	3	4	6	3	4	4	7	8	2	5	2	3	2	5	1	8	4	

Facial Width

Similarities Between Species

+ indicates significance at the 1% confidence level

CHAPTER IX

CONCLUSIONS

Brain patterns in Hybopsis may vary in configuration and/or size. The functional significance of configurational differences between species or infraspecific populations (H. aestivalis) is not demonstrable. Changes in configuration and relative size of some brain lobes were noted as the specimen size increased. This may be due to changes in the available cranial space or to differential growth of the functional units of the central nervous system associated with transitions in behavior patterns occurring during ontogeny. Lachner (1950) pointed out slightly different habitat and food preferences between juvenile and adult Nocomis.

In contrast to configurational variations, size differences are usually attributable to functional adaptations. In some species, relative lobe size can be correlated with hyperdevelopment or degeneration of a specific afferent sensory system.

Previous workers have attempted to utilize brain patterns in constructing fish classifications. While these attempts have generally been unsuccessful, comparisons among higher taxa often show good phylogenetic differences. Miller and Evans (1965) stated that extreme caution must be exercised in using brain patterns alone to indicate phylogenetic affinities. They showed that brain patterns in Thoburnia rhothoeca and Pantosteus delphinus were similar because of parallelisms in habitat preference and feeding behavior, although they belong to different tribes of Catostominae.

Intrageneric morphological differences among species of Hybopsis are usually rather subtle, particularly if no functional significance can be directly attributed to the characteristic. Even in a speciose, highly-variable genus such as Hybopsis most differences can be directly attributed to some functional adaptation in behavior or for a particular habitat. However, there are noticeable differences which cannot be immediately attributed to such adaptations. For example, forebrain lobes are long and thin in H. rubrifrons and thick and short in H. gracilis. This situation apparently results from differences in snout length and available space between the eyes. A balanced taxonomic evaluation of Hybopsis based on brain patterns should utilize specimens from all parts of the range of each species. Where material was available, the brain pattern within a species was reasonably stable, although slight configurational differences among species populations from different areas existed. This was not true in H. aestivalis, however. The difficulty of separating infraspecific variation from interspecific variation, in concert with problems associated with ontogenetic variation, preclude strict use of brain patterns as taxonomic characters at the species level. In Hybopsis, therefore, the most significant use of comparative brain morphology lies in providing insight into sensory specializations in various species and infraspecies populations.

Fishes with enlarged vagal lobes have generally been shown to be bottom feeders with large numbers of buccal and pharyngeal taste buds and have been designated as "mouth tasters" (Evans, 1931). Sight-feeding fishes usually have enlarged optic and small facial and vagal lobes. However, *H. hypsinota*, *H. amblops* and *H. rubrifrons* have large optic lobes and well-developed vagal lobes, while *H. insignis* has a large facial lobe and well-developed optic lobes. Fishes with enlarged facial lobes have abundant cutaneous taste buds and have previously been designated as "barbel tasters" (Satô, 1941) or "skin tasters" (Evans, 1952). Miller and Evans (1965) suggested adoption of the term "skin taster" because many fishes with enlarged facial lobes do not have barbels.

Although all *Hybopsis* usually possess barbels, the small barbel size and paucity of taste buds in some species disputes their utility as a feeding apparatus. Based on the length of the barbel and density of taste buds, barbels must certainly be considered useful in *H. aestivalis*, *H. gelida* and possibly *H. labrosa*.

Methods of sorting and concentrating food items in the buccal and pharyngeal cavities are apparently extremely variable in *Hybopsis*. In general, sight-feeding fishes have many deep longitudinal fods in the lining of the buccal cavity, while species from turbid waters have fewer and lower longitudinal folds. Behavioral observations of a sight-feeding species, *H. biguttata*, suggest that fishes with numerous deep folds are able to discriminate and sort food items in the buccal cavity. Since taste buds are sparse in this area, it is probable that this ability is attributable to tactile receptors. Konishi and Zotterman (1963) showed that fibers of the palatine nerve respond selectively to mechanical stimulation. These fishes usually feed on macroscopic animals having a different texture than nonfood items. Conversely, fishes with numerous taste buds in the branchial region do not appear to sort food in the buccal cavity. Behavioral observations of *H. storeriana* and *H. aestivalis australis* revealed a sustained "chewing motion" after which expulsion of material was noted. Regardless of the mode of initial food location, it is probable that these fishes often ingest quantities of fine detrital material with food items. Even in fishes with numerous, deep, longitudinal folds, sorting of fine particles may not be possible mechanically and must be done in the more chemically sensitive branchial cavity. Feeding mechanisms of an obligatory sight feeder, *H. crameri*, or an efficient "skin taster", *H. gelida*, are not difficult to envisage. However, intergradation of sensory mechanisms between these spectral end points creates difficulty in visualizing the types of interaction occurring among the various systems.

With some exceptions, brain patterns are relatively uniform within a subgenus. The marked distinctiveness of *H. labrosa* suggests that it has either diverged from the adaptive pattern established by other members of the subgenus *Hybopsis*, or that it may not actually be as closely related, phylogenetically, as the present classification indicates. *H. gelida* and *H. meeki* have very similar brain patterns but different gustatory mechanisms, while apparently residing in similar habitats. It is probable that they are filling very different ecological niches within the habitat. Brain patterns and gustatory mechanisms in *Extrarius* also exhibit differences which can be correlated with habitat-types.

According to Hutchinson (1957), "... in any large group of sympatric species belonging to a single genus or subfamily, careful work will always reveal ecological differences." By developing differences in food habits, feeding behaviors and habitat preferences, competition among sympatric species of fishes may be prevented or reduced. The

Powell River of Tennessee has six species of *Hybopsis* in a short stretch of the stream: *H. aestivalis hyostomus*, *H. amblops*, *H. cahni*, *H. dissimilis*, *H. insignis* and *H. micropogon*. The area contains a diversity of habitats: riffles, pools, backwaters, and a wide channel with a sand or gravel bottom. Although the food habits of these fishes are not known, the branchial cavities of all six species contained abundant algae, primarily diatoms and desmids. It is not known if the algae was actively selected or taken while securing animal food. However, examination of the brain patterns and gustatory apparatus reveal three types of feeding mechanisms, typified by *H. amblops*, *H. dissimilis* and *H. insignis* (discussed above). Feeding mechanisms of *H. aestivalis*, *H. cahni* and *H. micropogon* are similar to those of *H. dissimilis*, but these species appear to prefer different microhabitats in the stream. *H. dissimilis* is found in swift water at the base of riffles, *H. aestivalis* in moderate currents over fine gravel and sand, and *H. micropogon* in moderate currents over large gravel. The preferred habitat of *H. cahni* is unknown. It is likely that among at least five, and probably all six, of these species direct competition is avoided or buffered in some manner.

Based on the brain patterns and taste bud distribution, *Hybopsis* can be divided into three rather diffuse groups.

Group I, "sight feeders," consists of *Nocomis*, *Erimystax*, *Oregonichthys*, *Couesius* and perhaps *H. labrosa* and certain clear-water subspecies of *Extrarius*. Fishes of this group basically have large optic lobes and moderate numbers of external and internal taste buds. Divergences from the basic pattern which have been cited usually can be shown to be adaptations to a specific mode of feeding.

Group II, "skin tasters," consists of *Platygobio*, *Macrhybopsis* and silty-water subspecies of *Extrarius*. Reduction of the optic lobes and enlargement of the facial lobes with an increase in cutaneous taste buds are characteristic. An increase in internal taste buds accompanies the preceding characters, except in *H. gelida*.

Group III, "mouth tasters," contains all members of the subgenus *Hybopsis*, except *H. labrosa*. These fishes are characterized by large numbers of internal taste buds and enlarged vagal lobes. The number of cutaneous taste buds and optic lobe size are variable, perhaps indicating different methods of locating food.

Numerous publications point to a gradual deterioration of water quality in the continental United States. Industrial and domestic pollution is increasing rapidly in some areas while water quality in others is being degraded by an increase in turbidity. Although many rivers are now extremely turbid, citations by Moore (1950) indicated that many of these streams have been muddy for a long time. Undoubtedly, careless agricultural practices have succeeded in increasing former turbidity levels. Available habitats of some sight and taste-feeding species of *Hybopsis* have been drastically curtailed by increased siltation or other pollutants (Trautman, 1957; Deacon and Metcalf, 1961).

The prevailing governmental practice of reservoir construction on large rivers creates another perplexing problem. Sedimentation of suspended solids in the reservoirs clears streams below the dams, reducing the available habitat for fishes adapted for turbid waters (three to five Jackson units in the Red River below Lake Texoma) (U. S. Dept. of Health, Education and Welfare, 1962). These areas may be potential habitats for clear-water species of Hybopsis, but the dams and reservoirs may prevent access to these waters.

Paradoxically, the taste buds which allow some Hybopsis to survive in turbid waters may lead to their reduction or extinction. Bardach, Fujiya and Holl (1965) found that exposure to 0.5 ppm detergents (alkyl benzene sulfonates) for a period of approximately 24 days was sufficient to destroy 50 per cent of the taste buds of Ictalurus natalis. Length of time for regeneration was not determined but four to six weeks was not sufficient. Higher concentrations, 10 ppm, destroyed 50 per cent of the taste buds in one day. Concentration in many major rivers was reported at 0.1 to 0.2 ppm (Orsanco, 1963), while the detergent level was reported higher than 0.5 ppm in the Illinois River for 150 miles below Chicago (Hurwitz et al., 1960). The problem of increasing pollution partially results from the manufacture of branched-chain detergents which are not readily degraded by stream bacteria as are single-chain detergents.

Fishes such as Hybopsis meeki and H. gelida are adapted for existence in turbid streams and frequently exhibit a degenerate visual system. Further increases in detergent levels would place fishes reliant on chemical stimuli at a serious disadvantage and may ultimately cause drastic reduction in populations.

CHAPTER X

SUMMARY

1. Observations were made on 394 specimens in 21 nominal species of the genus Hybopsis. Morphometric data were taken from four body and 16 brain areas. Serial sections of the head of selected specimens from each species were used for histological examination and enumeration of internal and external taste buds. Morphometric data were analyzed by use of a digital computer.

2. Line drawings of the brains were prepared from a selected representative of each species for comparative purposes.

3. Functional anatomy of the brain and sensory mechanisms involved in feeding among teleosts are discussed. The distribution and habitat and food preferences are listed for each species, where known.

4. Feeding behaviors and habitat preferences are postulated for little-known species by comparing gustatory mechanisms and brain patterns with well-known species. Behavioral observations on three species tend to verify inferences of feeding habits based on morphological observation.

5. Fishes inhabiting turbid waters usually have the greatest numbers of cutaneous taste buds, often accompanied by numerous internal taste buds, reduced optic lobes, flattened tori and enlarged facial lobes and valvula.

6. Fishes inhabiting clear waters basically locate food by sight. There is, however, a broad spectrum of mechanisms for sorting food items. Most sight-feeding species show a paucity of taste buds (external and internal), while others (subgenus *Hybopsis*) apparently are "mouth tasters" with abundant internal taste buds and enlarged vagal lobes.

7. Total taste bud numbers increase with fish size.

8. Variability in brain lobes is greatest in those fishes inhabiting the most variable habitats.

9. Intrageneric brain pattern studies are most useful in determining dominant sensory modalities. Within the basic cyprinid brain plan, size and conformation of brain lobes are so intimately related to functional specializations that convergence or divergence are extremely difficult to ascertain without resorting to use of other, hopefully more stable, characters. This virtually precludes exclusive use of this character in systematic evaluations, and such have been avoided in the text of this paper.

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