TULANE STUDIES IN ZOOLOGY AND BOTANY

VOLUME 21
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TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY AND BOTANY, a publication of the Biology Department of Tulane University, is devoted primarily to the biology of the waters and adjacent land areas of the Gulf of Mexico and the Caribbean Sea, but manuscripts on areas outside this geographic area will be considered. Each number contains an individual monographic study or several minor studies. Normally two numbers plus an index and a table of contents are issued annually. Preferred citation of the journal is *Tulane Stud. Zool. and Bot.*

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TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 21, Number 1 $4.00 Feb. 1, 1979

A BIBLIOGRAPHY OF LOUISIANA BOTANY
1951-1975

ERIC SUNDELL

TULANE UNIVERSITY
NEW ORLEANS

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I saw in Louisiana a live-oak growing,
All alone stood it, and the moss hung down from the
branches;
Without any companion it grew there, uttering joyous
leaves of dark green,
And its look, rude, unbending, lusty, made me think of
myself
But I wonder'd how it could utter joyous leaves, standing
alone there, without its friend, its lover near —
for I knew I could not;
And I broke off a twig with a certain number of leaves
upon it, and twined around it a little moss,
And brought it away—and I have placed it in sight
in my room;
It is not needed to remind me as of my own dear
friends,
(For I believe lately I think of little else than of them:)
Yet it remains to me a curious token—it makes me
think of manly love;
For all that, and though the live-oak glistens there in
Louisiana, solitary, in a wide flat space,
Uttering joyous leaves all its life, without a friend, a
lover, near,
I know very well I could not.

Walt Whitman, 1860

TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 21, Number 1 $4.00 Feb. 1, 1979

A BIBLIOGRAPHY OF LOUISIANA BOTANY
1951 – 1975

ERIC SUNDELL

Department of Biology, Tulane University,
New Orleans, Louisiana 70118

This bibliography was undertaken to supplement Joseph Ewan's original "Bibliography of Louisiana Botany" (1968) which compiled references through 1950. The format and style followed here represent an extension of that work. Reprinting of the original bibliography, now virtually unavailable, would of course greatly enhance whatever value the supplement might have, not only because it would spare the reader an unnatural disjunction in the story of Louisiana botany, but because it would conveniently allow contemporary workers and students a comparison with the character and achievements of the past. Such a reprinting is not now under consideration.

The present bibliography includes titles on the algae, fungi, bryophytes, and vascular plants of the state of Louisiana and its coastal waters. Most entries fall into the realms of floristics and plant taxonomy, on the one hand, and plant ecology or environmental analysis, on the other. References from diverse branches of botanical literature are assembled, with the focus on the natural flora and vegetation of the state. Thus, horticultural and agricultural items are excluded unless, like the rich literature on the Louisiana irises, they treat largely of plants growing without cultivation - originally, at least - within our boundaries. Forestry is included only when it contains significant redeeming botanical qualities! General monographs are also out-of-bounds, unless locally pertinent floristically or historically — type material from our area, for instance, is grounds for incorporation. Unpublished theses and dissertations, despite valuable field data that so many carry, are omitted. Occasional citations of works not listed in this bibliography (e.g. Viosca, 1935) refer to Ewan's 1967 bibliography. In addition, a number of pre-1951 items that are not found in the original Louisiana bibliography are entered here. Although effort was made to examine all references, a few were missed; these are marked with an asterisk, and, if annotated, the source of the information is cited. Finally, the bibliography is indexed by author, subject, and botanical name.

I wish to express my gratitude to Joseph Ewan on several counts: for suggesting this project, in the first place, for the many references he passed on to me; for his critical reading of the manuscript; and, above all, for the various tools and tricks of the bibliographer's trade that he generously shared with me.

EDITORIAL COMMITTEE FOR THIS PAPER:
DR. JOSEPH EWAN, Professor Emeritus, Tulane University, New Orleans, Louisiana 70118

1863.* [1] Reizenstein, L. von. Catalogue of the Lepidotera of New Orleans and its vicinity. New Orleans: Issac T. Hinton. 8 p.

The oldest catalogue of these pollinators for our area, but according to Lambremont, 1954, the basis for the author's determination of species in unknown.

1873.* [2] Hilgard, E.W. Supplementary and final report of a geological reconnaissance of the State of Louisiana made under the auspices of the New Orleans Academy of Science and the Bureau of Immigration, May and June, 1869.

See originally, Hilgard, 1869. According to Cain, 1974, a copy of the supplement is to be found at University of Mississippi Library, Mississippi Collection.

1875. [3] Maitre, R. Illustrated and descriptive catalogue of vegetable and flower seeds, Holland or Dutch bulbs, tuberous and perennial plants, green-house, hot-house and bedding plants, ornamental and evergreen trees, flowering shrubbery, camelias and roses, garden implements, and other garden requisites. Philadelphia. [Private printing]. 129 p.

Seed store was located at 631 Magazine Street and the nurseries and green-houses at 976 Magazine, in New Orleans. An impressive variety of edibles and ornamentals, (18 palms and 64 "orchids or parasites") are offered for sale. Bulbs and roots were annually imported from Holland, but much of the rest was "exclusively our own product" and consequently "thoroughly to our climate." Illustrations rather few and eclectically borrowed.

1878. [4] Chapman, A.W. An enumeration of some plants – chiefly from the semitropical regions of Florida – which are either new, or which have not hitherto been recorded as belonging to the flora of the Southern States. Botan. Gaz. 3:2-6, 9-12, 17-21.

Half a dozen plants from New Orleans, chiefly Josiah Hale's collections, are among the new records.

1888. [5] Albrecht, J. The palms. A physiognomic sketch. Trans. Amer. Hort. Soc. 5:98-108.

Pantropical discussion by a widely travelled Louisiana resident. One or two local examples drawn upon.

1888. [6] Renauld, F. and J. Cardot. New mosses of North America. I. Botan. Gaz. 13:197-203.

Fontinalis flaccida collected by Langlois in East Louisiana, "in the branches and roots overflowed in the Bayou Bonfouca" (St. Tammany Parish). (Plate XIX). Part II, *ibid.* 14:91-100. Here tallied several other of Langlois' mosses, some of them new records for North America. See also item 323.

1895. [7] Muller, J. Graphideae Eckfeldtianae in Louisiana et Florida, lectae, additis obervationibus in Graphideas Calkinsianas ejusdem regionis. Bull. Herb. Boiss. 3:41-50.

Lichens from St. Martinville (St. Martin Parish) and Pointe a la Hache (Plaquemines Parish), the collections of Father Langlois. According to Dix (1945), the lichens were sent by Eckfeldt, cuator at the Acad. Nat. Sci. Phila., to Muller for identification. They are credited to Eckfeldt but carry Langlois' collection numbers. About 45 species, 12 of them newly described. See Briquet, J., *Biographies des Botanistes a Geneve* (1940), for a life of Muller, who was curator for the de Candolles.

1896. [8] Renauld, F. and J. Cardot. Musci Americae septentrionalis exsiccati. Notes sur quelques especes distribuees dans cette collection. Bull. Herb. Boiss. 4:1-19.

New Louisiana records are based upon collections of Father Langlois.

1899. [9] Bicknell, E. Studies in *Sisyrinchium* – I: Sixteen new species from the southern states. Bull. Torrey Botan. Club. 26:217-231.

S. furcatum, the only specimens cited are from Hammond, Tangipahoa Parish, in southeastern Louisiana.

1900. [10] Anon. [Note of A.B. Langlois' death.] Botan. Gaz. 30:359.

1901. [11] Lloyd, F.E. A botanical reconnaissance of the Mississippi Sound islands and delta. J. New York Botan. Gard. 2:26-29.

Brief observations on the vegetation of the islands lying between Biloxi, Mississippi, and the Mississippi Delta, and of the Delta proper.

1904. [12] Lloyd, F.E. The delta of the Mississippi. J. Geogr. 3:204-213.

Observations were made during a botanical reconnaissance in summer of 1900 (see Lloyd, 1901). Botanical annotations. Six photographs.

1923. [13] Huxley, J.S. Ils n'ont que de l'ame: an essay on bird-mind. *In* Essays of a biologist, pp. 105-130. New York.

It was on the Louisiana coastal plain, at McIlhenney's bird sanctuary on Avery Island (Iberia Parish), that the impassioned courtship and nesting rituals of the Louisiana heron and the "little White Egrets" made a lasting impression on this great English biologist. Anhingas and egrets at play are also among the recollections. Botany minimal.

1926. [14] Abbott, E.V. A survey of the microbiological activities in some Louisiana soils: a preliminary survey. La. State Univ., Agr. Exp. Sta., Bull. No. 194. 25 p.

According to Hodges, 1962, one of the earliest surveys for soil fungi (among other things) in the southern states.

1928. Pessin, L.J. Mycorrhiza of southern pines. Ecology 9:28-33.

[15] Ectotrophic mycorrhiza of *Pinus echinata, P. palustris, P. taeda,* and *P. caribaea* studied at Bogalusa (Washington Parish). Seven figures.

1931. Small, J.K. and E.J. Alexander. Botanical interpretation of the iridaceous
[16] plants of the Gulf States. Contrib. New York Botan. Gard. 327.

"Excerpt from the forthcoming *Manual of the Flora of the Southeastern United States,*" which includes our Florida Parishes. 96 species of *Iris*, 75 of which are new binomials from southern Louisiana. Viosca later (1935) reduced these to four species.

1931. Viosca, P., Jr. Spontaneous combustion in the marshes of southern Louisi-
[17] ana. Ecology 12: 439-442.

In our enlightenment we may no longer believe in the death of Dickens' Mr. Krook by spontaneous combustion, but the author's interpretation of the more than 100 marsh fires in question is intriguing and convincing.

1932. Viosca, P., Jr. Irises of Louisiana. Flower Grower 19:386-387.
[18] The earliest of Viosca's iris publications and a popular forerunner of his definitive taxonomic and ecological study that appeared in 1935. See also Penn, 1962.

1933. de Lesdain, B. Lichens de la Louisiane recueillis par les frères G. Arsène et
[19] Néon. Ann. Crypt. Exot. 6:49-58.

Introduction in French by Frère Arsène, followed by a list of Arsène's Covington collections (St. Tammany Parish) and Néon's from Lafayette. Three new species are described. Also an annotated list of lichens collected by Langlois, determined by l'abbé Hué and published in his *Lichenes Extra Europaei*.

1935. Brown, C.A. Notes on the distribution of an epiphytic orchid, *Epidendrum*
[20] *conopseum* Ait. in Louisiana. Proc. La. Acad. Sci. 2:105-106.

Brief survey of the literature and parish list of collections known to the author.

1935. Brown, C.A. Some wildflowers of Louisiana. La. Conserv. Rev. 4(5):3-7, 44.
[21] First in a series of eight, 1935, '36, '37: II. Woodland flora of the pine flats. *ibid.* 4(6):18-24; III. Flora of the alluvial soils. *ibid.* 4(7):22-29; IV. Trees, shrubs, and vines. *ibid.* 4(8):32-37; V. Ferns and fern allies. *ibid.* 5(1):12-23; VI. Weeds of Louisiana. *ibid.* 5(3):19-24; VII. Poisonous plants. *ibid.* 5(4):34-39; VIII. Four spring flowers. *ibid.* 6(1):10-11. In all, a popular running account for the outdoorsman, illustrated with sketches and photographs. First report of the introduction of *Caperonia castaneaefolia* into Louisiana from the tropics, VI, p. 23, most likely a misidentification. No voucher mentioned.

1935. Russell, R.J. and H.V. Howe. Cheniers of southwestern Louisiana. Geogr.
[22] Rev. 25:449-461.

Long narrow sandy ridges along the Gulf Coast, called "cheniers" by the Creoles because of the great live oaks that thrive in their well-drained, fertile soil. Paper treats of the Quaternary origin of these formations, a contest between subsidence and delta growth. "Origin of Cameron Marsh" (Cameron Parish), pp. 454-456. Two maps, three photos.

1937.* Frye, T.C. and L. Clark. Hepaticae of North America. Univ. of Wash. Publ.
[23] Biol. 6(1-5):1-1018.

1937 to 1947. Early Louisiana contributions by such noted hepaticologists as Alexander Evans, Marshall A. Howe, and L. M. Underwood tabulated. 65 species designated from Louisiana. *Koch, 1961.*

1939. Svihla, R.D. Field notes on a collection of Louisiana Hepaticae. Bryologist
[24] 42:118-120.

About 20 new records for the state, taken in the marshlands near Morgan City (St. Mary Parish).

1940. Grout, A.J. Moss notes, 1939. Bryologist 43:74-76.
[25] Range extensions into Louisiana for *Leucobryum antillarum* and *Polytrichum piliferum*, based on collections of Faith Pennebaker [Mackaness].

1942. Brown, C.A. History of the wild strawberry in Louisiana. Home Gardening
[26] 2:168, 174, 180.

The author tracks the elusive wild strawberry of Louisiana, a plant mentioned by Bartram and Rafinesque, Riddell, Langlois and Small, his quest ending successfully on Silver Creek, Washington Parish, with the rediscovery of *Fragaria grayana (F. virginica)*. Brown's motive for this eleven year search was largely philanthropic rather than botanical: to improve our cultivated variety of strawberry by crossing with the native.

1942. Brown, C.A. Native orchids. Home Gardening 3:6-7, 20.
[27] Popular article with information on distribution, especially of *Epidendrum conopseum*.

1942. Foote, L.B. Bibliography of the official publications of the state of Louisiana,
[28] 1803-1934. American Imprints Inventory No. 19. 576 p.

Issued by Hill Memorial Library at Louisiana State University as part of the WPA Historical Records Survey Program. Publications of La. State Univ., Agr. Exp. Sta. and Agr. Ext. Div., may be found pp. 347-393, but are of extremely limited value for our purposes. 1935-1948 comprises vol. I of "State of Louisiana, Official Publications," also compiled by L.B. Foote. Vol. II. 1948-1953, compiled by M.T. Lane. Both volumes appeared in 1954. 1954-1972, Vols. III, IV, and V, are, as stated on the title pages, compiled by W.O. Martin, Jr., Secretary of State, but the more likely candidate is M.T. Lane who remains Recorder of Documents throughout that period. A separate series began in 1949 as "State of Louisiana, Public Documents," appearing biannually and consecutively numbered (no volumes). These numbers are periodically superceded by the volumes of "Official Publications." More recent publications of the Agricultural Experiment Station, the Wild Life and Fisheries Commission, and the Forestry Commission are often of botanical interest.

1942. Mackaness, F.P. Bryophytes of the live oak forest. [Abstract.] Proc. La.
[29] Acad. Sci. 6:48-49.

A rich abundance of corticolous bryophytes characterizes the live oak forest association. Mention of seven species.

1942. [30] Prescott, G.W. The fresh-water algae of southern United States II. The algae of Louisiana, with descriptions of some new forms and notes on distribution. Trans. Amer. Microsc. Soc. 61:109-119.

Annotated list of some 60 taxa.

1942. [31] Russell, R.J. Flotant. Geogr. Rev. 32:74-98.

Flotant is a fitting subject for geographers as well as botanists, for the conversion of open water into marsh creates a zone half plant, half land, a natural process in southern Louisiana that alligator-weed and water-hyacinth have only accelerated. Development and anatomy of flotant is emphasized, but the article will serve as a serious introduction to the entire subject, botanically, geographically, and culturally.

1943. [32] Brown, C.A. Opportunities for paleobotanical research in Louisiana. Proc. La. Acad. Sci. 7:36-38. "1942."

Synopsis stresses study of lignite, the richest source of information on past vegetation in Louisiana. See also Brown, 1954.

1944. [33] Eyles, D.E., J.L. Robertson, Jr., and G.W. Jex. A guide and key to the aquatic plants of the southeastern United States. U.S. Public Health Bull. No. 286. 151 pp.

Reprinted 1963 by U.S. Dept. Interior, Fish and Wildlife Serv., as Bureau of Sport Fisheries and Wildlife Circular 158. "Southeastern" U.S. officially bounded on the west by the Mississippi-Louisiana line. Illustrated keys to genera and species and annotated species lists. A fairly rigorous guide, but without full species descriptions it is of limited value beyond genus. Supt. of Documents No. I 49.4:158.

1944. [34] Kane, H.T. Deep delta country. New York. 283 p.

The account of A.B. Langlois' years as priest at Pointe a la Hache (Plaquemines Parish) where, only a few years before his arrival, his predecessor, Father Savelli, had been killed by a furious mob, is rich in botanical anecdotes: overcoming the problem of drying specimens in so humid a place, for instance – "Callers at the rectory during the worst days of July found a hot fire in the living room, and Father covered with perspiration as he worked at the hearth." And parishioners coming to mass from the back canals and lakes, proudly bearing plants for Father. pp. 228-234. The author acknowledges the Right Reverend Monsignor Joseph Langlois (p. 271) for hitherto unpublished material regarding his uncle, Father Langlois. Other sources are not indicated, though a lengthy "Selected Bibliography" lends added reliability to Kane's account of "the Botanist-Priest of Plaquemines."

1945. [35] Cook, M.T. Species of *Synchytrium* in Louisiana. I. Description of species found in the vicinity of Baton Rouge. Mycologia 37: 284-294.

Part one in a series of eight, (1945, '47, '49, '51, '52, '53): *Mycologia* 37:571-576, 37:715-740, 39:351-357, 41:24-27, 43:103-107, 44:827-828, 45:101-114. *Synchytrium* is a genus of gall forming parasites of higher plants. Part III: Development and structure of the galls. The other seven entries contribute to a state roster of some 40 species, the vast majority of which are newly described. Most speciments were collected around Baton Rouge. See also several follow-up articles of John Karling for supplementary data and some taxonomic adjustments.

1945. Dix, W.L. Langlois' Louisiana Cladoniae. Bryologist 57:156-159.

[36] The collection forming the basis of this report resides at the National Museum in Washington, D.C. Langlois wrote in the preface to his *Catalogue*, "It is hoped in a future new edition to give also a list of the lichens of the region." Apparently he never did so. Biographical sketch and history of the lichen specimens make this a particularly valuable contribution. See also Müller, 1894, and Tucker, 1970.

1946.* Brown, C.A. and W.H. Carter. Weed investigations. La. State Univ., Agr.
[37] Exp. Sta., Bull. No. 402. 24 p.

1946. Taft, C.E. Some Oedogoniaceae and Zygnemataceae from Texas and Louisi-
[38] ana. Trans. Amer. Microsc. Soc. 65:18-26.

Nineteen taxa recorded for the state from collections between Shreveport and Baton Rouge. *Oedogonium louisianense* sp. nov. from Reeves, Allen Parish.

1947. Earle, T.T. The flowering cycle of water hyacinth. Proc. La. Acad. Sci.
[39] 10:27-29.

New Orleans study. Timetable of opening and closing of flowers, with related data.

1947. Lynch, J.J., J.E. King, T.K. Chamberlain, and A.L. Smith. Effects of aquatic
[40] weed infestations on the fish and wildlife of the Gulf States. U.S. Dept. Interior, Fish and Wildlife Serv., Spec. Sci. Rep. No. 39. 71 p.

Supt. of Documents No. I 49.15:39. Almost exclusively water-hyacinth and alligator-weed. Appendix A: "Investigations of the effects of the water-hyacinth on the fish and fish habits of Louisiana waters," esp. pp. 30-51.

1947. Robinson, B.B. Minor fiber industries. Econ. Botan. 1:47-56.

[41] Spanish-moss gatherers in Louisiana, working the bayous for fallen moss, may average 500 pounds per day! *Spartina* "grass" as a substitute for broom corn. Saw palmetto.

1948.* de las Barras y de Arago, Francisco. Cuando la Luisiana era espanola! Una
[42] remesa de plantas. Montes 4:126-131. [USDA Botany Subject Index 14019].

1948. Olive, L.S. Taxonomic notes on Louisiana fungi – I. Mycologia 40:6-20.

[43] Several new genera and species of parasitic fungi found in the state, in addition to new distributional and host records *Thallospora* gen. nov. (*T. aspera* on *Veronica peregrina*) and Heicomina gen. nov. (*H. caperoniae* on *Caperonia castaneaefolia*). But see Item 21). All collections from Baton Rouge.

1948. Olive, L.S. Taxonomic notes on Louisiana fungi – II. Tremellales. Mycolo-
[44] gia 40:586-604.

27 species of jelly fungi, 4 of which are previously undescribed.

1949. Bodman, M.C., Sr. The genus *Heterochaete* in the United States. Mycologia
[45] 41:527-536.

H. sublivida Pat. is known only from the type locality at St. Martinville, where it was collected by Langlois in 1897. The genus was previously unknown in the United States. *H. andina*, the other species in our area, is more widespread. Four figures.

1949. Viosca, P., Jr. Natural checks on the water-hyacinth. Proc. La. Acad. Sci.
[46] 12:67-71.

A more comprehensive article than the title indicates. Senescence of water bodies, the result of flotant or large permanent mats of water-hyacinth and many native and introduced aquatic weeds, is here considered the consequence of drainage and flood control measures. Solid observation and comprehension make of this plea for rejuvenation of bayous, swamps, and canals of the low country a solemn warning about Louisiana's future natural health.

1950. Jung, R.C. An annotated list of the Lepidoptera of the New Orleans area.
[47] Proc. La. Acad. Sci. 13:42-48.

A few cultivated plants identified as larval hosts.

1950. Moore, W.G. Limnological studies of Louisiana lakes. I. Lake Providence
[48] [East Carroll Parish]. Ecology 31:86-99.

"Aquatic Vegetation" discusses briefly the unanticipated paucity of the higher aquatic flora of this hard-water lake. "Plankton": primarily blue-greens, greens and diatoms.

1950. Scott, A.M. New varieties of *Staurastrum ophiura* Lund. Trans. Amer.
[49] Microsc. Soc. 69:248-253.

Var. *horridum* only in Louisiana; var. *longiradiatum*, La., Miss. and Fla.

1951. Boudreaux, B.H. The insect family Aphididae in Louisiana. Proc. La. Acad.
[50] Sci. 14:14-22.

List of species includes the known plant hosts in the state.

1951. Brown, C.A. Cypress – the tree unique: the wood eternal. Garden J. New
[51] York Botan. Gard. 1:36-39.

General information on the ecology and uses of baldcypress. Photographs of several extraordinary trees.

1951. Cooke, M.T. Distribution of species of *Synchytrium* in North America.
[52] Mycologia 43:590-597.

Fourteen spp. described by the author from material collected in our area. That Louisiana is the *Synchytrium* center of America reflects Cook's intensive work in his own state and a paucity of collections elsewhere. "...possibly all species found in America have a much wider geographical distribution than has been reported." No bibliography.

1951. Fassett, N.C. *Callitriche* in the New World. Rhodora 53:137-155, 161-182,
[53] 185-194, 209-222.

Louisiana collections of Langlois cited: *C. terrestris, C. nuttallii, C. peploides* var. *peploides, C. heterophylla* var. *heterophylla*. Drummond's collection of *C. peploides* from New Orleans probably isotype of *C. drummondi*, and Hale's Louisiana collection of *C. nuttallii* cited by Hegelmaier as an isotype. Key to southeastern species. Maps and crucial illustrations.

1951. Flint, L.H. Some winter red algae of Louisiana. Proc. La. Acad. Sci. 14:34-
[54] 36.

A few freshwater species discussed.

1951. Olive, L.S. Taxonomic notes on Louisiana fungi. III. Additions to the Trem-
[55] ellales. Mycologia 43:677-690.

Fifteen species of jelly fungi, most of which represent new records for the state. Several new species described.

1951. Penn, G.H. A brief chronology of the history of entomology in Louisiana.
[56] Proc. La. Acad. Sci. 14:72-87.

Excellent bibliography. Many entries with botanical information.

1951. Shinners, L.H. The North Texas species of *Hymenocallis* (Amaryllidaceae).
[57] Field and Lab. 19:102-104.

Pancratium liriosome Raf. (in *Florula Ludoviciana*) = *Hymenocallis liriosome* (Raf.) Shinners. *H. eulae*, here newly described from only Texas, has subsequently been found in Louisiana.

1952. Brown, C.A. Notes on the occurrence of *Ophioglossum crotalophoroides*
[58] Walt. in Louisiana. Amer. Fern J. 42:90-92.

Evidently common on lawns in the Baton Rouge area and easily overlooked. No mention of vouchers. One figure, no scale.

1952. Gleason, H.A. The new Britton and Brown illustrated flora of the northeast-
[59] ern United States and adjacent Canada. New York and London. 3 vols.

Like Fernald's edition of Gray's *Manual*, this monumental flora of the northeast remains of inestimable service to southern botanists. The fit with our Louisiana flora is perhaps best for the upland oak-hickory hardwoods of East and West Feliciana and East Baton Rouge parishes and for coastal plain elements. Second and third printings, 1958 and 1963, both slightly revised.

1952.* Horn, N.L. A comparative study of two species of *Colletotrichum* on vetch.
[60] Phytopathology 42:670-674.

C. sativum described as a new species on *Vicia* spp. and *Pisum sativum* in Louisiana. *Biol. Abst.*

1952.* Langdon, O.G., M.L. Bomhard, and J.T. Cassady. Field book of forage

[61] plants on longleaf pine-bluestem ranges. U.S. Forest Serv., Southern Forest Exp. Sta., Occ. Pap. 127. 117 p.

1952. Penfound, W.T. Southern swamps and marshes. Botan. Rev. 18:413-446.
[62] "Systematic" study of the major types of swamps and marshes of the Southeast with in-depth discussion of each. Lengthy bibliography.

1952. Phaff, H.J., E.M. Mrak, and O.B. Williams. Yeasts isolated from shrimp.
[63] Mycologia 45:698-719.

Thirty-five cultures of yeasts were isolated from shrimp (*Penaeus setiferus*) collected in the Gulf of Mexico off the coast of Texas.

1952. Shanor, L. The characteristics and morphology of a new genus of Laboulbe-
[64] niales on an earwig. Amer. J. Botan. 39:498-504.

Filariomyces forficulae, collected in Baton Rouge. 25 figures, including photomicrographs.

1953. Cook, T. Louisiana irises, a bibliography. Lafayette: Southwestern Louisiana
[65] Institute. 16 p.

"This is not a complete bibliography, but it is the first printed work that shows what has been written on Louisiana Irises." Two pages of newspaper items are particularly valuable.

1953. Duncan, W.H. Taxonomic collections of vascular plants in the southeastern
[66] states – their abundance and relation to production of floras. Rhodora 55:353-358.

Dot map, based on published records of five genera, indicates relatively poorly collected areas: most of Mississippi, Louisiana, and Tennessee. Table compares all southeastern states: only Miss. scores lower than La. in "Corrected Average Number of Collections per County."

1953. Exner, B. Comparative studies of four rhizoctonias occurring in Louisiana.
[67] Mycologia: 45:698-719.

Pathogens of considerable importance on beans, sugar cane, rice, figs. Pathology and taxonomy.

1953. Flint , L.H. Two new species of *Batrachospermum*. Proc. La. Acad. Sci.
[68] 16:10-15.

Batrachospermum mikrogyne Flint et Skuja and *B. basilare* Flint et Skuja, two freshwater red algae described and, thus far, known only from Louisiana. Voucher specimens filed at 6 herbaria, including LSU & US.

1953. Greene, W.F. and H.L. Blomquist. Flowers of the South, native and exotic.
[69] Chapel Hill, North Carolina. 208 p.

An informative rather than merely descriptive text accompanies useful line drawings (floral details wanting) to some 400 native and 100 exotic plants. 55 color plates, accenting the horticultural, include many excellent and ambitious artistic compositions remarkable for their botanical accuracy. La. well represented in the many "Fla. to Texas" species.

1953. Karling, J.S. *Micromyces* and *Synchytrium*. Mycologia 45:276-287.
[70] "Many of the new species created by Cook [see item 35] will have to be reinvestigated thoroughly."

1953. Karling, J.S. *Synchytrium urticae*. Mycologia 45:613-615.
[71] Invalidity of Cook's binomial and discussion of its possible identity with some Russian *Synchytria*.

1953. Karling, J.S. *Synchytrium chamaedryoidis*. Mycologia 45:976-977.
[72] Cook's = *S. urticae*, though an invalid name, is confirmed as a true species, and a nomenclatural change is proposed.

1953. Lowy, B. *Auricularia* in Louisiana. Proc. La. Acad. Sci. 16:28-30.
[73] " ... to clarify and summarize briefly our knowledge of this genus in the state." Three species considered.

1953. Lowy, B. Myxomycetes of Louisiana. Mycologia 45:926-933.
[74] Checklist includes 42 new reports for the state. Collections from Baton Rouge. Ten figures.

1954. Bick, G.H. A bibliography of the zoology of Louisiana. Proc. La. Acad. Sci.
[75] 17:5-48.

Reflects author's interest in the literature of "Natural history," thus indirectly of even greater use to botanists than a stricter treatment. Headings include "Climate, Geology, Physiography" and "Major Vegetation Studies."

1954. Brown, C.A. Palynological studies on Louisiana lignite. [Abstract.] Internat.
[76] Botan. Cong. Proc. 8(6):270.

Fifty outcrops of Tertiary lignite are rich in pollen and fern spores. Correlations suggested between these grains and grains described from Eocene brown coals of Germany.

1954. Drechsler, C. Some Hyphomycetes that capture eelworms in southern states.
[77] Mycologia 46:762-782.

Two of the new species of nematode-capturers collected in Laplace (St. John the Baptist Parish), Louisiana.

1954. Drechsler, C. Two species of *Conidiobolus* with minutely ridged zygospores.
[78] Amer. J. Botan. 41:567-575.

C. rhysosporus and *C. osmodes* new species found in decaying plant detritus from southern Louisiana. Close observation of spores and spore germination. Four pages of figures.

1954. Flint, L.H. *Sirodotia* in Louisiana. Proc. La. Acad. Sci. 17:59-65.
[79]
Freshwater red algae closely allied to *Batrchospermum* and favoring cold, swift-flowing streams. Six species collected from Louisiana to date.

1954. Karling, J.S. The galls of *Synchytrium modioliensis*. Bull. Torrey Botan. Club
[80] 81:199-209.
Originally described by Cook from Baton Rouge [35] and apparently collected earlier by Langlois (1888) in the state. A few details of interest concerning the Langlois collection filed at NY.

1954. Karling, J.S. *Synchytrium brownii*, a new species with sexual reproduction.
[81] Sydowia 8:27-30.
Established for a parasite of *Oenothera laciniata* in Louisiana and named for Clair A. Brown in appreciation of his help collecting species of *Synchytrium*. However, see Karling, 1958.

1954. Karling, J.S. *Synchytrium modioliensis* Cook and *Synchytrium australe* Speg-
[82] azzini. Mycologia 46:529-533.
Cook's parasite collected on *Modiola caroliniana* from Baton Rouge is synonymous with Spegazzini's Argentinian species. The latter has priority.

1954. Lambremont, E.N. The butterflies and skippers of Louisiana. Tulane Stud.
[83] Zool. 1:127-164.
Botanical commentary, mostly larval-feeding habits, scattered throughout. References include several other Louisiana Lepidoptera titles.

1954. Lowy, B. A new *Dacrymyces*. Bull. Torrey Botan. Club 81:300-303.
[84]
D. nigrescens, a jelly fungus, from the Baton Rouge area. Eleven figures.

1954. Lowy, B. A new species of *Platygloea* from Louisiana. Mycologia 46:100-104.
[85]
P. longibasidia on frondose wood, Goodwood, La. Believed to represent "a primitive ancestral type from which the rusts could conceivably have been derived."

1954. Lytle, S.A. and B.N. Dirskell. Physical and chemical characteristics of the
[86] peats, mucks and clays of the coastal marsh area of St. Mary Parish, Louisiana. La. State Univ., Agr. Exp. Sta., Bull. No. 484. 37 p.
Foldout map of soil types. Information on water-holding capacity and organic matter patently of great use to wetlands ecologists.

1954. Penn, G.H. Introduced pitcher plant mosquitoes in Louisiana (Diptera,
[87] Culicidae). Proc. La. Acad. Sci. 17:89-90.
Scarcity of *Sarracenia purpurea* in Louisiana is apparently the critical factor preventing permanent establishment of *Wyeomyia haynei* Dodge.

1954.* [88] Stroube, W.H. Host range of the *Rhizoctonia* aerial blight fungus in Louisiana. Plant Dist. Reporter 38:789-790.

List of the natural plant hosts of *Pellicularia filamentosa* f. *sasakii*. *Biol. Abst.*

1954.* [89] Stroube, W.H. *Puccinia oahuensis* on *Digitaria ischaemum* and *D. sanguinalis* in Louisiana. Plant Dist. Reporter 38:120.

Apparently the first record of this rust fungus in Louisiana, and the first record of its occurrence on *D. ischaemum*. *Biol. Abst.*

1954. [90] Taylor, W.R. Sketch of the character of the marine algal vegetation of the shores of the Gulf of Mexico. U.S. Dept. Interior, Fish and Wildlife Serv., Fishery Bull. 89:117-192.

Louisiana algal flora, pp. 187-188. Extensive bibliography. Supt. of Documents No. I 49.27:89. Bull. 89 is devoted entirely to the Gulf of Mexico and includes other pertinent titles: Phytoplankton, pp. 163-169; Bacteria, Fungi, and Unicellular Algae, pp. 217-232. See also Thorne, 1954.

1954. [91] Thorne, R.F. Flowering plants of the waters and shores of the Gulf of Mexico. U.S. Dept. Interior, Fish and Wildlife Serv., Fishery Bull. 89:193-202.

Literature review yields four principal communities of flowering plants: submarine meadow, mangrove swamp, salt marsh, sand-strand vegetation. Floristic and ecological synopsis with extensive bibliography. Supt. of Documents No. I 49.27:89.

1954.* [92] Wolff, S.E. A guide to plant names in Texas. Oklahoma, Louisiana, and Arkansas. Rev. by C.A. Rechenthin. U.S. Dept. Agr., Soil Conserv. Serv. 91 p.

1955. [93] Anon. Forests of Louisiana, 1953-1954. U.S. Forest Serv., Southern Forest Exp. Sta., Forest Survey Release 75. 64 p.

Brief descriptions of forest types. Colored maps showing 5 forest types and "non-typed, less than 10% forest." *Egler, 1961*

1955. [94] Anon. Publications of the Southern Forest Experiment Station, July 1921 through December 1954. U.S. Forest Serv., Southern Forest Exp. Sta., Occ. Pap. 108 (Revised). 128 p.

Numerous valuable titles for the plant ecologist, especially in the areas of grazing and fire ecology, can be had here by selective culling. An understanding of fire ecology is no doubt the key to an understanding of the vegetation of the coastal plain, a vast sub-climax zone of pine, and it is our state and federal agencies that have the funds and manpower to investigate the role of fire, botanically as well as commercially. Reprints are often available on request to S.F.E.S. in New Orleans. See also Punch, 1962.

1955.* Benjamin, R.K. New genera of Laboulbeniales. Aliso 3:183-197.
[95] *Homaromyces* newly described from Illinois and Louisiana: *H. epieri* parasitic on a beetle. *Biol. Abst.*

1955. Drechsler, C. Additional species of Zoopagaceae subsisting on Rhizopods and eelworms. Mycologia 47:364-388.
[96] Four more types (see item 77) from Laplace (St. John the Baptist Parish).

1955. Eggler, W.A. Radial growth of nine species of trees in southern Louisiana. Ecology 36:130-136.
[97] Based on 70 trees, March to March 1951-1952. Two areas, riverfront in Jefferson Parish and cypress-tupelo swamp in St. Charles Parish. *Egler, 1961.*

1955. Hansford, C.G. Tropical fungi. V. New species and revisions. Sydowia 9:1-88.
[98] Among the many new descriptions of spp. and vars., find (p. 3) *Irenopsis quercifolia* on *Quercus*, Louisiana and Florida. Herbarium study.

1955. Karling, J.S. *Synchytrium ranunculi* Cook. Mycologia 47:130-139.
[99] Originally described as a parasite of *Ranunculus pusillus* at Baton Rouge. Life cycle with 31 figures.

1955.* Lowy, B. Illustrations and keys to the tremellaceous fungi of Louisiana. Lloydia 18(4):149-181.
[100] Nine species. *Speairs and Lowy, 1957.*

1955. Lowy, B. Some Louisiana Gasteromycetes. Proc. La. Acad. Sci. 18:45-53.
[101] Keys to orders, families, genera, and species, followed by a checklist of 32 species, 28 of which represent first reports from the state. Eleven photographs help to compensate for the lack of full species, habitat and substrate descriptions.

1955. Wherry, E.T. The identity of *Dupratzia* Rafinesque. Castanea 20:71.
[102] The genus *Dupratzia*, first proposed by Rafinesque in his *Florula Ludoviciana* of 1817, is formally placed on record as a later name for *Eustoma* Salisbury, (Gentianaceae), the "West Indian bluebell." (*Index Kewensis* refers *Dupratzia*, with a question, to *Phlox*).

1955. Wilbur, R.L. A revision of the North American genus *Sabatia* (Gentianaceae). Rhodora 57:1-33, 43-71, 78-104.
[103] Tulane herbarium consulted. Type of *S. macrophylla* Hook. var. *microphylla* collected by Drummond in St. Tammany Parish. *S. brachiata*: Louisiana collections by Drummond, Arsene, Cocks. *S. grandiflora*: single Louisiana collection, by Josiah Hale, filed at Gray. *S. brevifolia*: also a single state collection, at MO, without locality data: " ... should not be included in flora of the state without a better substantiated record." Louisiana vouchers for several other species are numerous.

1956. Blake, S.F. The identity of *Calyptocarpus blepharolepis*. Rhodora 58:275-278.
[104]

Some history of *C. vialis*'s eastern march from Texas across Louisiana and some New Orleans collections.

1956. Breen, R.S. and R.A. Pursell. More mosses from Stone Mountain, Georgia and vicinity. Bryologist 59:184-186.
[105]

"Specimens of *Splachnobryum* collected by Faith Pennebaker Mackaness in New Orleans are *S. wrightii*, a species closely related to *S. bernoullii*." This collection of an uncommon, tropical American moss, was published originally as *S. bernoullii*. See also Koch, 1957.

1956. Brown, C.A. Commercial trees of Louisiana. Baton Rouge: Louisiana Forestry Commission. 76 p.
[106]

Paperback. Seventy species described and illustrated with photographs: bark, leaves, fruits or flowers. Interesting tidbits. Map of tree regions divides state into six vegetation regions.

1956. Gunter, G. Land, water, wildlife and flood control in the Mississippi Valley. Proc. La. Acad. Sci. 19:5-11.
[107]

Careful summary and interpretation of a subject that will always be at the heart of the natural history of Louisiana. The fate of once natural overflow areas currently deprived of both floodwater and its alluvium is one of several topics considered.

1956. Humm, H.J. Sea grasses of the northern Gulf Coast. Bull. Mar. Sci. Gulf and Carib. 6:305-308.
[108]

Observations and collections in Mississippi Sound off Ocean Springs, Miss. Annotated list of six species with key.

1956. Karling, J.S. Undescribed species of *Synchytrium*. Mycologia 48:83-98.
[109] *S. nitidum* collected by Clair Brown on *Specularia (Triodanis) biflora* at Baton Rouge.

1956. Koch, L.F. Louisiana muscology 1. Review and summary of literature. Bryologist 59:192-203.
[110]

Details of collectors and collections within the state (Drummond, Featherman, Mohr, Langlois, et al.) and subsequent history of the collections and their incorporation into catalogues of broader geographic range. Louisiana citations are culled from a diffuse literature, making the literature cited surely the most complete and useful list to date for Louisiana bryologists. Two appendices: doubtful Louisiana taxa and *nomina nuda* and other rejected reports.

1956. Lowy, B. A note on *Sirobasidium*. Mycologia 48:324-327.
[111] *S. sanguineum* Lager. & Pat. found on a dead branch of *Fraxinus nigra* near Baton Rouge. Few records for this genus in North America, and this and Olive's 1951 report are our only local collections of the species.

1956. [112] Mackin, J.G. *Dermocystidium marinum* and salinity. Proc. Natl. Shellfish Assoc. 46:116-128.

A parasite of oysters studied in Redfish Bay (Plaquemines Parish), Louisiana. The genus is hanging in Ainsworth and Bisby's *Dictionary of the Fungi*, "? Chytridiales or Protozoa."

1956. [113] Moore, J.A. Notes on fern distribution in Louisiana. Amer. Fern. J. 46:82-84.

Localities in northern Louisiana additional to Brown and Correll, 1942. Six ferns and *Selaginella apoda*.

1956. [114] Moore, J.A. *Silene virginica* in the Gulf States. Rhodora 58:27-29.

Reported by Riddell, 1852, and later by Dormon, 1934, as occurring in Louisiana, but not upheldin Hitchcock and Maguire's revision of North American species of *Silene* (1947). Vouchers from four parishes.

1956. [115] Penfound, W.T. Primary production of vascular aquatic plants. Limnol. Oceanogr. 1:92-101.

Comparison of primary production in vascular aquatics with that of several terrestrial communities emphasized the high productivity of the former. Data on productivity of water-hyacinth supplied by T.T. Earle from a New Orleans population.

1956. [116] Plakidas, A.G. *Cercospora* leaf spot of *Abelia*. Mycologia 48:382-385.

A parasite of the popular ornamental shrub, *Abelia grandiflora*, is described: *Cercospora abeliae* sp. nov. from Baton Rouge.

1956. [117] Schuster, R.M. Notes on Nearctic Hepaticae X. A study of *Cephaloziella rhizantha, C. ~~floridae~~* and *C. ludoviciana.*

Langlois collected the type of *C. ludoviciana* in 1888 in St. Martinville. Here incorporated in *C. rizantha*.

1956. [118] Shinners, L.H. *Euthamia pulverulenta* Greene (Compositae) in southeastern Louisiana. Field and Lab. 24:38.

1956. [119] Shinners, L.H. *Forestiera autumnalis* Buckley (Oleaceae) in eastern Texas and western Louisiana. Southwestern Nat. 1:87-88.

"Though adequately described as long ago as 1863 (*Proc. Acad. Nat. Sci. Phila.* 14(1862):7), from 'Eastern Texas and Western Louisiana', this very distinct species has never been included in any flora or list." New collection from Sabine Parish (sterile material).

1956. [120] Shinners, L.H. *Hypochoeris glabra* L. (Compositae) in Arkansas and Louisiana. Southwestern Nat. 1:88.

1956. Shinners, L.H. *Physostegia serotina* (Labiatae), a new species from coastal
[121] Louisiana and Texas. Field and Lab. 24:17-19.

Type from Calcasieu Parish. Key to the eight species of *Physostegia* occurring in the "Gulf Southwest."

1956. Shinners, L.H. *Tragia smallii* Shinners, sp. nov. Field and Lab. 24:37.
[122] *T. betonicaefolia* sensu Small. Paratype from Vernon Parish.

1956. Shinners, L.H. Yellow-flowered *Oxalis* (Oxalidaceae) of eastern Texas and
[123] Louisiana. Field and Lab. 24:39-40.

"Though often quite weedy, all the *Oxalis* of eastern Texas ... and Louisiana are, in my opinion, undoubtedly native." Three species distinguished; one new variety described.

1956. Sternitzke, H.S. and J.A. Putnam. Forests of the Mississippi Delta. U.S.
[124] Forest Serv., Southern Forest Exp. Sta., Forest Survey Release 78. 42 p.

Brief descriptions of forest types. No map of forest types. *Egler, 1961.*

1956. Ware, G.H. Vegetational zonation on a Red River sand bar near Natchi-
[125] toches [Natchitoches Parish], Louisiana. Proc. La. Acad. Sci. 19:21-24.

An obscure aerial view supplements this short discussion of a periodically flooded habitat.

1956. Wilson, H.R. Louisiana bryophytes. Bryologist 59:17-21.
[126] Excellent prelude to Koch's more comprehensive Louisiana review published the same year. Wilson includes liverworts and adds a list of some fifty species collected in a baldcypress-tupelo gum swamp in Tangipahoa Parish, of which many are first reports for the state.

1957. Bandoni, R.J. The spores and basidia of *Sirobasidium*. Mycologia 49:250-
[127] 255.

Recharacterization of the genus based in part upon a Lowy collection of *S. sanguineum* from near Baton Rouge.

1957. Brown, C.A. Check list of woody plants of Louisiana, native, naturalized,
[128] and cultivated. Baton Rouge, La. Forestry Comm., Bull. No. 8. 16 p.

Pamphlet. Second edition appeared in 1959, 76 p., 71 figs. Fourth edition in 1964 as La. Forestry Comm. Bull. 10. 80 p.

1957. Deiler, F.G. Vegetation management of storage water reservoirs at Garden
[129] Island Bay [Plaquemines Parish]. Proc. La. Acad. Sci. 20:24-35.

A massive invasion of vegetation (*Phragmites, Typha, Zizaniopsis, Alternanthera, Eichhornia*) and the chemical counterattack documented with excellent tables on species, species aggregations, herbicide treatments and effects. Nutria cited as a natural check on water-hyacinth.

1957.* [130] Dillon, O.W. Food habits of wild ducks in the rice-marsh transition area of Louisiana. Proc. Ann. Conf. Southeast Assoc. Game and Fish Comm. 11: 114-119.

1957. [131] Glasgow, L.L. and A. Ensminger. A marsh deer "die-off" in Louisiana. J. Wildlife Mgmt. 21:245-247.

Gulf marshes, Vermilion and Iberia Parishes. With information on vegetation types, site types, and extensive vegetation change related to a 1952 salt water inundation. *Egler, 1961.*

1957. [132] Hardin, J.W. Studies in the Hippocastanaceae, IV. Hybridization in *Aesculus*. Rhodora 59:185-203.

A. glabra X *pavia* has been collected in Bossier Parish.

1957. [133] James, C.W. Notes on the cleistogamous species of *Polygala* in southeastern United States. Rhodora 59:51-56.

P. polygama forma *obovata* elevated to *P. crenata*, the type collected in New Orleans, Drummond 1832.

1957. [134] Koch, L.F. Louisiana muscology 2. The herbarium of Tulane University, New Orleans. Brittonia 9:96-71.

Twenty-one taxa are added to the known flora of the state, mostly the collections of Penfound and F.P. Mackaness.

1957. [135] Lowy, B. A new *Exidia*. Mycologia 49:899-902.

Type from Baton Rouge.

1957. [136] Rock, H.F.L. A revision of the vernal species of *Helenium* (Compositae). Rhodora 59:101-116, 128-158, 203-216.

Southeastern genus with Louisiana representatives. Drummond and Arsene collections of *H. vernale*, a Joor collection of *H. brevifolium* from Slidell (St. Tammany Parish), 1887, and a Ball collection of *H. flexuosum* from near "Alexander" (Rapides Parish). *H. drummondii* is endemic to Texas-Louisiana coastal plain.

1957. [137] Shinners, L.H. *Polygonum bicorne* Raf. instead of *P. longistylum* Small. Rhodora 59:265-267.

"... the much abused Rafinesque ...," "The special condemnation of the *Florula Ludoviciana* ...," "... the lie that the descriptions were scrappy and inadequate has been monotonously repeated by persons who never saw Robin's 3-volume book ..." More than a defense, this is a counterattack.

1957. Shinners, L.H. *Wahlenbergia marginata* (Thunb.) A. D.C. (Campanulaceae)
[138] in Louisiana. Southwestern Nat. 2:44.

A single small plant was found on a roadside in Rapides Parish. As Shinners predicted, it is now a common roadside weed in many parts of the state.

1957. Speairs, R.K., Jr. and B. Lowy. Notes on *Tremella* in North America. Proc.
[139] La. Acad. Sci. 20:83-84.

Of 19 North American species, 10 have been found in Louisiana. History of collections and species list for the state.

1957. Wherry, E.T. Reminiscences of John K. Small. Castanea 22:126-129.
[140]

Among the memorable anecdotes: Wherry's discovery that Small was color-blind – colonies of bright red clinopodiums or castilleias looked gray to him. Their discovery of the "Louisiana Irises," now internationally celebrated, while waiting for the Lake Pontchartrain ferry-boat to be repaired – they had hoped to be in New Orleans for lunch.

1958. Chabreck, R.H. Beaver-forest relationships in St. Tammany Parish, Louisi-
[141] ana. J. Wildlife Mgmt. 22:179-183.

Plot sampling along streams occupied by beaver revealed that beaver used 22 woody plant species, (tabulated). *Liquidambar styraciflua, Magnolia virginiana, Pinus glabra*, and *P. taeda* received the most use. During summer months beaver fed heavily on roots and basal portions of herbaceous plants, esp. *Leersia*. Excellent and intriguing study. Literature cited contains a few related titles for our area.

1958. Clark, L. *Frullania gymnotis* found in the United States. Bryologist 61:67.
[142]

Three widely separated localities. The Louisiana material was collected in 1926 and reported by Svihla as *F. obcordata* in 1939.

1958. Dormon, C. Flowers native to the deep South. Baton Rouge: Claitor's Book
[143] Store. 176 p.

Updates nomenclature of *Wild Flowers of Louisiana*, 1942, yet still no authorities cited. 33 color plates (registery often blurred) and 100 excellent line drawings, all by the author. Accurate and with all the fringe benefits of an informal catalogue.

1958. Gleason, H.A. Two new stations for *Carex picta*. Rhodora 60:175.
[144]

Rare sedge first discovered near New Orleans by Drummond. New stations in Mississippi.

1958. Harris, V.T. and R.H. Chabreck. Some effects of Hurricane Audrey on the
[145] marsh at Marsh Island [Vermilion Parish], Louisiana. Proc. La. Acad. Sci.
21:47-50.

5400 foot line transect through a *Spartina patens – Scirpus olneyi* marsh. The island lies in Vermilion Bay.

1958. Karling, J.S. *Synchytrium fulgens* Schroeter. Mycologia 50:373-375.
[146] Cook's Louisiana collection: identified as *S. fulgens*, renamed *S. brownii* by Karling in 1954, restored to *S. fulgens*: what one physiologist has superciliously called the Taxologic Cycle.

1958. Lowy, B. Anomalous phalloids. Mycologia 50:792-794.
[147] From Baton Rouge.

1958. Maisenhelder, L.C. Understory plants of bottomland forests. U.S. Forest
[148] Serv., Southern Forest Exp. Sta., Occ. Pap. 165. 40 p.

Thirty-six plants identified and illustrated with rather washed-out photographs. Especially for the Mississippi delta.

195 Ownbey, G. Monograph of the genus *Argemone* for North America and the
[149] West Indies. Torrey Botan. Club Mem. 21(1):1-159.

Identity of Rafinesque's *A. alba* from Louisiana, pp. 138-140. For earlier discussion of same, see Prain, D., 1895, "An account of the genus *Argemone*," *J. Botan*. 33:330.

1958. Pursell, R.A. Discovery of *Solmsiella kurzii* in Louisiana. Bryologist 61:366-
[150] 367.

On *Magnolia grandiflora*, Weeks Island (salt dome), Iberia Parish. The first collection of this minute, allegedly rare, liverwort-like moss outside the type locality in Florida.

1958. Shinners, L.H. *Carduus nutans* L. (Compositae), a European thistle in north-
[151] western Louisiana. Southwestern Nat. 3:220.

1958. Welden, A.L. Prodromus fungi ludovicianae. J. Tenn. Acad. Sci. 33:252-257.
[152] Ten species of resupinate Homobasidiomycetes classed within the Thelephoraceae from lower Louisiana. Emphasis is on microscopic characters which, at that date, had only recently gained ascendency over gross morphology as an index of true relationships. Several new records for the state. One figure.

1958. Wood, C.E., Jr. The genera of the woody Ranales in the southeastern United
[153] States. J. Arnold Arboretum 39:296-346.

This is both the introduction and the first contribution to a projected generic study of the seed plants of the Southeast (bounded by and including Arkansas and Louisiana on the west). "... the objectives are toward a review and reorganization of familial and generic lines ... and, especially, toward bringing together at least a part of the vast botanical literature which bears upon the plants of this rich area." We will not pursue the project through this bibliography but we do alert the reader to its existence and great usefulness.

1959. Bick, G.H. Contributions of Edward Foster to the biology of Louisiana. Proc.
[154] La. Acad. Sci. 22:8-17.

Foster's wide range of interests included microcrustaceans, insects, coins and medals, and, for our purposes, horticulture. Louisiana Society of Naturalists was organized in 1897 and Louisiana Entomological Society in 1920, both as a result of his efforts. Interesting tidbits about his friend, R.S. Cocks.

1959. [155] Chamberlain, J.L. Gulf Coast marsh vegetation as food of wintering water fowl. J. Wildlife Mgmt. 23:97-102.

Marsh food utilization, based on 1251 gizzard analyses, involving relative abundance of 24 plants, plus 25 others. Rockefeller Wildlife Refuge (Cameron Parish) of 86,000 acres. *Egler, 1961.*

1959. [156] Humm, H.J. and R.M. Darnell. A collection of marine algae from the Chandeleur Islands [St. Bernard Parish]. Univ. of Tex., Publ. Inst. Mar. Sci. 6:265-276.

St. Bernard Parish. Annotated list of 35 species and discussion of ecological and phytogeographic relations. Maps, table, and diagram of relative abundance in littoral zone.

1959. [157] Kimble, R.B. and A. Ensminger. Duck food habits in southwestern Louisiana marshes following a hurricane. J. Wildlife Mgmt. 23:453-455.

Comparison of the results of this study after with a similar study before the hurricane (Chamberlain, 1959) indicates a great difference in the food eaten by ducks. Description of gross hurricane damage to vegetation amplifies conclusions drawn from duck gizzards.

1959. [158] Lowy, B. and A.L. Welden. Synopsis of Louisiana polypores. Amer. Midl. Nat. 61:329-349.

Survey of polypores reported from the literature (Featherman and Langlois especially) and from authors' collections. Keys to genera and species, annotations and photographs of the more interesting species.

1959. [159] Lytle, S.A., B.E. Grafton, A. Ritchie, and H.L. Hill. Soil survey of St. Mary Parish, Louisiana. U.S. Dept. Agr., Soil Conserv. Serv. Soil Survey 1952(3). 45 p.

An ongoing, county by county, national undertaking, indexed as Supt. of Documents No. A 57.38, and then alphabetically by county (or parish). Essential ecological data, maps and tables.

1959. [160] Mullahy, J.H. Preliminary survey of the algal flora of the Chandeleur Islands [St. Bernard Parish]. Proc. La. Acad. Sci. 22:62-68.

A group of barrier islands protecting the southeastern marshlands of St. Bernard Parish. Twenty-seven species of green, brown, and red algae were collected, indicating that the islands may well contain Louisiana's best growth of marine algae. Good, compact bibliography. Author's abstract, "The algal flora of the Chandeleur Islands of Louisiana," appeared the same year in *Internat. Botan. Congr. Proc.* 9(2):275.

1959.* [161] Nelson, I.S. Louisiana irises. *In* L.F. Randolph, *ed.* Garden irises. pp. 227-235. Ithaca, New York.

1959. [162] Reese, W.D. *Syrrhopodon parasiticus* in the southern United States. Bryologist 62:182-186.

New state reports for Alabama, Mississippi and Louisiana.

1960. [163] Blair, R.M. Deer forage increased by thinning in a Louisiana loblolly pine plantation. J. Wildlife Mgmt. 24:401-405.

Quantitative analysis of herbaceous and woody forage and palatable browse proved production of understory vegetation was directly related to pine-thinning intensity. Application of course to the millions of acres in the south shared by deer and loblolly pine.

1960.* [164] Harmon, B.G., C.H. Thomas, and L.L. Glasgow. Waterfowl foods in Louisiana rice fields. North Amer. Wildlife Conf. Trans. 25:153-161.

1960. [165] Kubota, J., V.A. Lazar, and K.C. Beeson. The study of cobalt status of soils in Arkansas and Louisiana using the black gum as the indicator plant. Proc. Soil Sci. Soc. Amer. 24:527-528.

Nyssa sylvatica is a cobalt accumulator. *Biol. Abst.*

1960. [166] Plakidas, A.G. Angular leaf spot of *Magnolia*. Mycologia 52:255-259.

Disease and pathogen (*Isariopsis magnoliae*) newly described, on *M. grandiflora* from Folsom (St. Tammany Parish), Louisiana. (Later reduced to synonomy under *Cercospora magnoliae*, *Mycologia* 54:448-454).

1960. [167] Reese, W.D. *Psilotum* in Louisiana. Amer. Fern J. 50:269-270.

1960. [168] Shinners, L.H. *Ranunculus trilobus* (Ranunculaceae) in southern Louisiana: new to the United States. Southwestern Nat. 5:170.

1960. [169] Welden, A.L. The genus *Cymatoderma* (Thelephoraeceae) in the Americas. Mycologia 52:856-876.

The author resides in New Orleans, and many Louisiana citations document the study of this tropical and sub-tropical group.

1960. [170] Welden, A.L. Prodromus fungorum ludovicianorum II. J. Tenn. Acad. Sci. 35:231-237.

Eight of the ten species reported as new records for the state.

1961. [171] Crum, H. and L.E. Anderson. A new *Fissidens* from Louisiana. Bryologist 64:345-348.

F. kochii n. sp., Sarpy Wildlife Refuge, St. Charles Parish, about 15 miles northwest of New Orleans – a favorite haunt for Tulane botanists and zoologists. Four figures.

1961. [172] Darnell, R.M. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. Ecology 42:553-568.

Sources of primary organic matter, both autochthonous and allochthonous, include bacteria, phytoplankton, submerged and marsh vegetation.

1961. [173] Dean, B.E. Trees and shrubs in the heart of Dixie. Birmingham. 246 p.

This field guide may be the most engaging blend of the sacred and profane on the botanist's book shelf. 430 species are described, annotated, and illustrated with line drawings. Supplemental illustrations are many and range from useful photographs of living plants and herbarium specimens to a series of rather odd, unforgettable color plates, evidently the paintings of the illustrator, Forrest Bonner. His persimmons and pomegranates seem excerpted from a Cezanne still life, and the trumpet vine has the charm of a Matisse. Roland Harper aided with identification of some of the specimens and as a general fund of information to the author.

1961. [174] Dukes, G.H., Jr. Some tertiary fossil woods of Louisiana and Mississippi. [Abstract.] Amer. J. Botan. 48:540.

Collections of petrified wood made in Vernon, Sabine, and De Soto parishes. Four new species reported from the Louisiana material (not enumerated in the abstract).

1961.* [175] Eggler, W.A. Vegetation of the drainage basin of Grand Bayou Blue. *In* R.J. Russell, *ed.*, Louisiana coastal marsh ecology. pp. 1-23. La. State Univ., Coastal Stud. Inst., Tech. Rep. No. 14.

1961. [176] Eggler, W.A. and W.G. Moore. The vegetation of Lake Chicot [Evangeline Parish], Louisiana, after eighteen years of impoundment. Southwestern Nat. 6:175-183.

Comparison made to Penfound's study of the lake (1949) just following impoundment.

1961. [177] Egler, F.E. Cartographic guide to selected regional vegetational literature. — Where plant communities have been described. Part II. Southeastern United States. Sarracenia 6:1-87.

Annotated Louisiana bibliography and accompanying map, pp. 75-81, which have been of great service to this and to Ewan's original bibliography.

1961.* [178] Halls, L.K. and T.H. Ripley, eds. Deer browse plants of southern forests. U.S Forest Serv., Southern and Southeastern Forest Exp. Sta. 78 p.

Illustrated guide to identification of about 35 species or species groups, with some information on forage value and management. Accounts of the individual species were prepared by authorities from all parts of the South. *Punch, 1962.*

1961.* [179] Hoffpauir, C.M. Methods of measuring and determining the effects of marsh fires.|Proc. Ann. Conf. Southeast. Assoc. Game and Fish Comm. 15:142-160.

1961. Koch, L.F. Louisiana hepaticology. 1. A list of species. Bryologist 64:54-57.
[180]

Brief historical sketch precedes list of hepatics: Faith Pennebaker Mackaness, collector and curator, most important contributor to Louisiana hepaticology to date. (Koch worked mostly with collections at Tulane).

1961. Lemaire, R.J. A preliminary annotated checklist of the vascular plants of the
[181] Chandeleur and adjacent islands, St. Bernard and Plaquemines Parishes, Louisiana. Proc. La. Acad. Sci. 24:116-122.

The Chandeleurs are the easternmost remnants of an abandoned delta of the Mississippi River. 119 species, 93 genera, 39 families.

1961. Lemaire, R.J. A preliminary annotated checklist of the vascular plants of the
[182] marshes and included higher lands of St. Bernard Parish, Louisiana. Proc. La. Acad. Sci. 24:56-70.

In extreme southeastern Louisiana: more than 90% of the 617 square miles of land area of the parish is marsh. 280 species, 212 genera, 85 families. Habitat and abundance annotations.

1961. Lemaire, R.J. A range extension for *Parapholis incurva*. Rhodora 63:176-
[183] 177.

Freemason Island, St. Bernard Parish: a first record of this European grass on the Gulf Coast.

1961. Negus, N.C., E. Gould, and R.K. Chipman. Ecology of the rice rat, *Oryzo-*
[184] *mys palustris* (Harlan), on Breton Island [St. Bernard Parish], Gulf of Mexico, with a critique of the social stress theory. Tulane Stud. Zool. 8:93-123.

Island divided into five areas based on vegetational zonation. Description of Breton Island, pp. 95-98. Food habits, p. 109. Two photos, *Fimbristylis* and *Opuntia-Yucca* communities.

1961. Randolph, L.F., J. Mitra, and I.S. Nelson. Cytotaxonomic studies of Louisi-
[185] ana irises. Botan. Gaz. 123:125-133.

Karyotype analyses of *I. fulva*, *I. giganticaeruleu*, *I. brevicaulis*, the Abbeville Red population, and natural hybrids gave no evidence in support of Edgar Anderson's assumption of introgressive hybridization. See Randolph, 1966 and 1967.

1961. Reese, W.D. A contribution to the bryology of the southern United States.
[186] Bryologist 64:50-54.

Range extensions on the Gulf Coast for ten species of mosses, six representing new state records for Louisiana. Brief description, including noteworthy ferns and angiosperms, of Week's Island (Iberia Parish), one of the coast salt domes and the locality for three of the new mosses.

1961. Russell, N.H. Keys to Louisiana violets (*Viola*—Violaceae). Southwestern
[187] Nat. 6:184-186.

Two keys: spring (flowering) and summer (vegetative). Sixteen species.

1962. Daubs, E.H. The occurrence of *Spirodella oligorrhiza* in the United States.
[188] Rhodora 64:83-85.

New collections of this Asiatic aquatic from widely separated areas include two in Louisiana. New to the state.

1962. Glasgow, L.L. and H.A. Junca. Mallard foods in southwest Louisiana. Proc.
[189] La. Acad. Sci. 25:63-74.

The most important wild water fowl in the northern hemisphere. Grasses prove first in importance to mallards as well as to man. Four tables give exhaustive lists of plant materials, identified to species, taken from mallard crops. Related titles cited.

1962. Harrar, E.S. and J.G. Harrar. Guide to southern trees. New York, 709 p.
[190] Dover reprint of the original 1946 publication with updated nomenclature. Ungenerously illustrated and of minimal usefulness for difficult genera like oaks and hickories. Clair Brown supplied the authors with "botanical materials" from our region.

1962.* Harris, V.T. and F. Webert. Nutria feeding activity and its effect on marsh
[191] vegetation in southwestern Louisiana. U.S. Dept. Interior, Fish and Wildlife
Serv., Spec. Sci. Rep. – Wildlife No. 64. 53 p.

Supt. of Documents No. I 49.15/3:64.

1962. Hodges, C.S. Fungi isolated from southern forest tree nursery soils. Mycolo-
[192] gia 54:221-229.

45 fungi documented from Louisiana soils, the majority imperfects. *Gonytrichum macrocladium* a new record from soil in the U.S.

1962.* Jemison, E.S. and R.H. Chabreck. The availability of water fowl foods in
[193] coastal marsh impoundments in Louisiana. North Amer. Wildlife Conf.
Trans. 27:1-19.

1962. Nelson, I.S. Native Louisiana irises. Plants and Garden 18(1):62-63.
[194] *I. fulva*, *I. brevicaulis*, *I. giganticaerulea*, and their hybrids: culture, morphology, and breeding. *Biol. Abst.*

1962. Oliver, R.L. and W.H. Lewis. Chromosome numbers of *Sisyrinchium* (Irida-
[195] ceae) in eastern North America. Sida 1:43-48.

Vouchers for *S. albidum* Raf., *S. sagittiferum* Bickn., and *S. bermudiana* L. from Louisiana. We need all the help we can get with this genus!

1962. Penn, G.H. Percy Viosca Jr. – Naturalist. Tulane Stud. Zool. 9:234-237.
[196]

"... one of the last of America's great naturalists ... Viosca was an authority on the wild flowers of Louisiana, particularly the ecology and hybridization of irises ... In 1935 he publishes a lengthy article straightening out the taxonomic jumble in which hitherto a multitude of species had been described in Louisiana. After years of crossbreeding and countless observations in the wetlands his deduction that there were only four species of Louisiana irises was surprising, but remains undisputed by taxonomic botanists."

1962. [197] Penn, G.H. Bibliography of studies by P. Viosca, Jr. Tulane Stud. Zool. 9:239-242.

A chain of publications from 1915 to 1961 leaving no doubt that this was a naturalist of extraordinary scope.

1962. [198] Perdue, R.E., Jr., Two new varieties and a new combination in *Rudbeckia*, Rhodora 64:328-329.

R. nitida Nutt. var. *texana* Perdue var. nov. restricted to southeastern Texas and western Louisiana.

1962. [199] Punch, L.E. Publications of the Southern Forest Experimental Station, 1955 through 1961. U.S. Forest Serv., Southern Forest Exp.aSta., Occ. Pap. 108 (Supplement 1). 57 p.

This list supplements the 1955 revision of Occ. Pap. 108 [Item 94]. Supplement 2, 1962 through 1970, appeared in 1971. Publications from 1971 to present appear in annual lists. All entries are accompanied by brief abstracts, and, again, many excellent papers are available on request to the S.F.E.S. in New Orleans.

1962. [200] Shinners, L.H. Annual sisyrinchiums (Iridaceae) in the United States. Sida 1:32-42.

The major area for all three species is in eastern Texas and Louisiana. Doubtful or excluded names: *S. brownii* Small, named in honor of Prof. Clair A. Brown of Louisiana State University, equals *S. exile* Bicknell. Many Louisiana collections cited for all species and one hybrid.

1962. [201] Shinners, L.H. *Drosera* (Droseraceae) in the southeastern United States: an interim report. Sida 1:53-59.

Field observations in Louisiana and neighboring states. Collections from the state cited for *D. capillaris* Poiret, *D. annua* E.L. Reed, and *D. leucantha* Shinners, sp. nov. Contends with Carroll E. Wood, Jr. over recognition of *D. annua*.

1962. [202] Shinners, L.H. Evolution of the Gray's and Small's *Manual* ranges. Sida 1:1-31.

"Perhaps the first thing that strikes one about the historical record is the abundance of authors and floras in the North, and their paucity in the South – and the further strange fact that all three authors of Southern floras came from the North ... Plainly the reasons are not botanical." (The author, by the way, is Canadian). This brilliant and intriguing historical synopsis of botany in the North and South is required reading. And there are predictions for the future, too. Regrettably, one of Shinner's works-in-hand, a flora of the Gulf Southwest, which was to include Louisiana west of the Mississippi, never saw the light of publication.

1962. [203] Shinners, L.H. *Micromeria brownei* and its allies (Labiatae). Sida 1:94-97.

M. brownei var. *pilosiuscula* Gray. Collection from St. Bernard Parish, Louisiana, examined.

1962. [204] Shinners, L.H. *Ranunculus trachycarpus* (Ranunculaceae) in south central Louisiana: new to North America. Sida 1:104-105.

1962. [205] Shinners, L.H. *Siphonychia* transferred to *Paronychia* (Caryophyllaceae). Sida 1:101-103.

P. drummondii T. & G. added to Louisiana flora.

1962. [206] Shinners, L.H. Synopsis of *Collinsonia* (Labiatae). Sida 1:76-83.

What Briquet and Rafinesque have done, Shinners has undone, and restored *Collinsonia* to its pre-1897 limits. Louisiana collections cited for *C. serotina* Walter and *C. tuberosa* Michaux.

1962.* [207] Simmons, E.G. and W.H. Thomas. Phytoplankton of the eastern Mississippi delta. Univ. Tex., Publ. Inst. Mar. Sci. 8:269.

1963. [208] Ewan, J. Riddell's place in the phytography of Louisiana. [Abstract.] Amer. J. Botan. 50:634.

Systematic botanist, 1807-1865.

1963.* [209] Linnartz, N.E. Relation of soil and topographic characteristics to site quality for southern pines in the Florida parishes of Louisiana. J. Forestry 61(6):434-438.

Loblolly, slash, and longleaf pines and their preferred soils. Depth to least permeable layer in soil profile, percent sand, drainage, pH, and slope are the variables that prove most significant in relation to "site index." *Biol. Abst.*

1963. [210] Logan, L.A. A list of seed plants of Lincoln Parish, Louisiana. Proc. La. Acad. Sci. 26:18-32.

The parish lies in the shortleaf pine uplands of north central Louisiana. Background plus bare list: 381 genera in 114 families.

1963.* [211] McGinn, L.R. and L.L. Glasgow. Loss of waterfowl foods in rice fields in southwest Louisiana. Proc. Ann. Conf. Southeast Assoc. Game and Fish Comm. 17:30-34.

1963. [212] Owens, A.G., Jr. and S. Riche. *Monanthochloe littoralis* (Gramineae) in Louisiana. Sida 1:182.

1963. Richardson, A.L. Some monocotyledonous plants of East Baton Rouge
[213] Parish. Proc. La. Acad. Sci. 26:9-15.

Twenty-three species listed (grasses, sedges, rushes excluded) with full annotations.

1963. Shiflet, T.N. Major ecological factors controlling plant communities in Lou-
[214] isiana. J. Range Mgmt. 16(5):231-235.

Salinity of the free soil water and fluctuating water levels are the major factors that control plant communities in Louisiana's four and one-half million acres of marshlands. "All flesh is grass," is the text emphasized; manipulation of salinity and water levels to change plant composition to better fit a range livestock enterprise.

1963. Shinners, L.H. Southeastern records of *Stachys affinis (S. sieboldii)* and *S.*
[215] *floridana* (Labiatae). Castanea 28:44-46.

S. floridana is added to the flora of Louisiana by a specimen from Orleans Parish. Now (1977) a fairly common weed in gardens here in New Orleans. Perennial with white, moniliform tubers – very striking.

1963. Solymosy, S.L. Plants of the U.S.L. "In-Use" Arboretum. Lafayette. 40 p.
[216] Plant list is coded to map of U.S.L. campus, the "In-use" Arboretum.

1964. Barrett, E.R. Variations of summer fungi in soil areas in northeast Louisiana.
[217] Proc. La. Acad. Sci. 27:53-58.

Variations are quantitative, the only taxonomic distinction being Agaricales vs. Polyporales. Four general soil areas investigated: Coastal Plain, Mississippi Terrace and Loessial Hills, Flatwoods, Recent Alluvium; their distribution clearly mapped.

196 Crum H. and L.E. Anderson. Notes on *Physcomitrium collenchymatum*.
[218] Bryologist 67:350-355.

Several collections of Mackaness née Pennebaker, Mackaness, Koch, and Reese firmly enlist this little moss in the state flora.

1964. Gagliano, S.M. An archaeological survey of Avery Island [Iberia Parish]. La.
[219] State Univ., Coastal Stud. Inst. 76 p.

An evaluation of the extent of prehistoric occupation of this coast salt dome. Botanical material is slim, but discussion of geological conditions, past and present, has bearing on local phytogeography.

1964. Johnston, M.C. *Scirpus molestus* (Cyperaceae), sp. nov. from Arkansas,
[220] Louisiana, and Texas. Southwestern Nat. 9:310-312.

Previously mistaken for *S. koilolepis*, the type of which was collected in New Orleans.

1964. Lowy, B. *Pisolithus* in Louisiana. Mycologia 56:319.
[221] Infrequently reported from North America, *P. tinctorius* is in fact one of the commoner Gasteromycetes of our region.

1964. [222] Radford, A.E., H.E. Ahles, and C.R. Bell. Manual of the vascular flora of the Carolinas. Chapel Hill. 1183 p.

Much overlap naturally exists between the Carolina flora and ours, and, despite the fact that Louisiana fails to qualify as one of the "eight of the southeastern states outside the Carolinas" for purposes of range citations, the book is nonetheless possibly the most useful single up-to-date volume for our area in terms of coverage and cost. It is currently used at L.S.U. as text for the introductory plant taxonomy course. A good many taxa are illustrated with excellent line drawings. Keys are artificial and highly serviceable.

1964. [223] Reese, W.D. Notes on Louisiana mosses. Bryologist 67:206-209.

Part one of at least six entries (1964, '65, '67, '69, '72, '74): *Bryologist* 68:243-245, 70:124-125, 72:68-69, 75:95-97, 77:467-468. Additions and adjustments to the roster of Louisiana mosses, including many range extensions to the author's original state records.

1964. [224] Richardson, A.L. A botanical report of some Archichlamydeae of East Baton Rouge Parish. Proc. La. Acad. Sci. 27:21-39.

173 species in 97 genera and 31 families. Arrangement of families follows Engler and Prantl through the Umbelliferae. Full annotations.

1964. [225] Shinners, L.H. *Scutellaria thieretii* (Labiatae), a new species from coastal Louisiana. Sida 1:251-252.

Sp. nov. Holotype from Vermilion Parish; also collected from Cameron Parish. Shinners, a splitter, named this new skullcap for "an energetic and productive collector."

1964. [226] Shinners, L.H. Two youngias ("*Crepis japonica*": Compositae) introduced in the southeastern United States. Sida 1:386-388.

First reported from U.S. in Small's *Manual* as *Crepis* from only southern Louisiana. Several collections cited from the state for *Y. japonica* (L.) DC.

1964. [227] Thieret, J.W. Additions to the flora of Louisiana. Castanea 28:169-170. "1963."

Nine new species.

1964. [228] Thieret, J.W. *Fatoua villosa* (Moraceae) in Louisiana: new to North America. Sida 1:248.

From southeast Asia. First U.S. collection is not from Lafayette, however, but most likely New Orleans: G.P. DeWolf *s.n.* 11 Oct. 1950, Tulane Campus (NO). By 1977 a common garden weed in Lafayette and New Orleans, and how very unlike a mulberry!

1964. [229] Thieret, J.W. *Lysimachia japonica* (Primulaceae) and *Clinopodium gracile* (Labiatae) in Louisiana: new to the United States. Sida 1:249-250.

1964. [230] Thieret, J.W. More additions to the Louisiana flora. Sida 1:294-295.

Ten state records, including three *Cyperus* spp.

1965. [231] Dorman, C. Natives preferred. Baton Rouge: Claitor's Book Store. 217 p.

Native trees and flowers of the southeast, where they can and cannot be grown. Author, herself a Louisiana native, tempers her enthusiasm with a caution to "diggin' women and men" against immoderate and indiscriminate transplanting.

1965. [231A] Ewan, J. French naturalists in the Mississippi Valley. *In* J.F. McDermott. The French in the Mississippi Valley. pp. 159-174. Urbana.

Brothers Louis and Jean Prat, Le Page du Pratz, Joseph Lakanal, etc., and their La. travels noticed.

1965. [231B] Ewan, J., ed., Letters from Charles Sprague Sargent to Reginald Somers Cocks, 1908-1926. J. Arnold Arboretum 46:1-44, 122-159, 324-361, 411-444.

Sargent wrote to Cocks in 1911, from the Arnold Arboretum, "To show how poor we are in Louisiana plants I could not find this morning a Louisiana specimen of *Liquidambar* in our herbarium." Most fascinating are Sargent's struggles with collections (and taxonomy) of the tougher genera: willows, hawthorns, plums, oaks, basswoods, hickories. Reprinted as separate with change of paging the same year.

1965. [232] Lemmon, B.E. Notes on a recent collection of *Fissidens neonii*, Bryologist 68:325-331.

One of very few Louisiana endemics. The first reappearance of this moss since the original collection by Brother Neon in 1931 near Lafayette, which E.B. Bartram (1932) described as *Moenkemeyera*. Eleven figures.

1965.* [233] Livingstone, R., Jr. A preliminary bibliography with KWIC index on the ecology of estuaries and coastal areas of the Eastern United States. U.S. Dept. Interior, Fish and Wildlife Serv., Spec. Sci. Rep. – Fisheries No. 507. 352 p.

Supt. of Documents No. I 49.15/2:507.

1965. [234] Lowy, B. and W.B. Cooke. The 1960 Louisiana foray. Mycologia 57:478-483.

A good harvest for the Mycological Society of America: Myxomycetes, Ascomycetes, Basidiomycetes, and Fungi Imperfecti identified from 7 collecting localities near Baton Rouge. One new genus, *Gliocephalotrichum*, was described from the Tunica Hills area, West Feliciana Parish.

1965. [235] Reese, W.D. and B.E. Lemmon. A natural hybrid between *Weissia* and *Astomum* and notes on the nomenclature of the North American species of *Astomum*. Bryologist 68:277-283.

W. controversa X *A. ludovicianum*, in southern Louisiana.

1965. [236] Rougeou, C.L. A tribute to Professor Ira S. Nelson. La. Soc. Hort. Res. Monthly News Letter 6(12):54-56.

Professor of Horticulture at University of Southwestern Louisiana, who brought many new and rare species into cultivation, is remembered both as teacher and horticulturalist.

1965. [237] Solymosy, S.L. *Limnophila indica* (R.Br.) Druce (Scrophulariaceae) in Louisiana. Sida 2:175.

1965. [238] Sternitzke, H.S. Louisiana forests. U.S. Forest Serv., Resource Bull. SO-7. 31 p.

Volume in growing stock (trees at least 5 inches in diameter) has risen 43 percent for softwood and declined 20 percent for hardwood since the midfifties. Of value not for its botany, for it is pure and unregenerate forestry, but as a comprehensive state survey loaded with tabular data, it does allow botanists an intimate look at foresters' activities without our having to wire-tap.

1966. [239] Banks, D.J. *Paspalum minus* (Gramineae) in Louisiana and Mississippi. Rhodora 68:94-96.

New locations bridge the gap between Texas and Alabama stations. Diploid race indicated by new chromosome counts, $n=10$.

1966. [240] Grelen, H.E. and V. Duvall. Common plants of longleaf pine – bluestem range. U.S. Forest Serv., Southern Forest Exp. Sta., Res. Pap. SO-23. 96 p.

Descriptions and excellent botanical drawings of more than 80 understory species: *Andropogon* and *Panicum*, legumes and composites are the dominants. Notes on values for cattle and wildlife. An elegant field guide.

1966. [241] Kral, R. Eriocaulaceae of continental North America north of Mexico. Sida 2:285-332.

Tropical American family with outliers in southeastern U.S. *Eriocaulon decangulare*, *E. texense*, *E. compressum*, *Lachnocaulon anceps* on record for Louisiana, and others so close as to be suspected.

1966. [242] Kral, R. *Juncus capitatus* Weigel (Juncaceae) in Louisiana: new to the United States. Sida 2:390-392.

But see *Sida* 2:436 – "*Juncus capitatus* (Juncaceae) previously reported from the United States," for corrections.

1966. [243] Kral, R. Observations on the flora of the southeastern United States with special reference to northern Louisiana. Sida 2:395-408.

Emphasis on northern woodland elements. Approximately a dozen species new to the state may be sifted from a longer list, but almost all entries represent range extensions and elucidations.

1966. Kral, R. *Xyris* (Xyridaceae) of the continental United States and Canada.
[244] Sida 2:177-260.

A difficult genus of the Gulf and Atlantic Coastal Plains with about half of some twenty species native to the state. Many of the author's voucher specimens for another smears collected in Louisiana. Generously illustrated.

1966. Lemmon, B.A. An ecological and floristic study of the mosses of Lafayette
[245] Parish. Proc. La. Acad. Sci. 29:23-36.

Annotated checklist includes 91 taxa, of which 45 are reported as "firsts" for the parish. Four bryological habitats and their mosses described. Study based on collections of Brother Neon, William D. Reese, Correll and Correll, and the author.

1966. Lemmon, B.E. *Fissidens hyalinus* in Louisiana. Bryologist 69:241-243.
[246] Disjunct in Japan and eastern U.S. New to the state. One figure.

1966. Maples, R.S., Jr. and D.D. Lutes. A checklist of ferns in Lincoln Parish,
[247] Louisiana. Amer. Fern. J. 56:33-36.

16 species, 6 parish records. Annotations.

1966. Moore, W.G. Central Gulf States and the Mississippi Embayment. *In* David
[248] G. Frey, *ed.*, Limnology in North America. pp. 287-300. Madison, Milwaukee, and London. 734 p.

Arkansas, Louisiana, Mississippi, and Alabama, with emphasis on our area with its rich and varied network of inland waters. Vital background for students of aquatic botany. Map of major drainage systems, p. 289. Extensive references.

1966. Randolph, L.F. *Iris nelsonii*, a new species of Louisiana iris of hybrid origin.
[249] Baileya 14:143-169.

Known locally as the Abbeville Reds, the assumed parental species of this stable hybrid are *I. fulva* and *I. giganticaerulea*. In-depth cytogenetic and morphological analysis with discussion of hybridization and introgression. Excellent photographs of plants and habitats.

1966. Reese, W.D. *Barbella pendula* (Sull.) Fleisch., a review of its distribution and
[250] comments on related species. Bryologist 69:208-213.

Type locality Lafourche Parish. Occurring in China and Japan, Mexico and in the United States only in Louisiana where it was first collected by Riddell. W.S. Sullivant described it as *Meteorium* in 1856 in ed. 2 of Gray's *Manual*. Two figures.

1966. Rickett, H.W. Wildflowers of the United States. II. The southeastern states.
[251] 2 vols. New York. 688 p.

241 folio-size, color plates (each with 6 or 7 separate photos) and numerous text figures make this the most sumptuous of modern wildflower picture books. Woody plants excluded, but many obscure herbs normally passed over are admitted and illustrated. Clair Brown is among the collaborators.

1966. Society for Louisiana Irises. 25th anniversary publication. Lafayette. 51 pp.
[251A] Reminiscence of John K. Small, a tribute to Ira S. Nelson, and Caroline Dorman's History of the Louisiana Iris make this a valuable botanical contribution.

1966. Solymosy, S.L. Poisonous plants. La. Soc. Hort. Res. Monthly News Letter
[252] 7(3):1-22.

Annotated, well-informed list of both native and cultivated plants from our area. As herbarium curators know well, public inquiries on this subject generally outnumber all others.

1966. Stuckey, R.L. The distribution of *Rorippa sylvestris* (Cruciferae) in North
[253] America. Sida 2:361-376.

Evidence for an introduced status includes two Louisiana collections of 1885: W.B. Waite's from Orleans Parish (US) and A.B. Langlois' from Plaquemines Parish (MICH).

1966. Stuckey, R.L. *Rorippa walteri* and *R. obtusa* synonyms of *R. teres* (Crucifer-
[254] ae). Sida 2:409-418.

Other synonyms include *Nasturtium micropetalum* Fischer and Meyer and *N. obtusum* Nuttall, holotypes from in and near New Orleans. Photograph of a portion of the latter, from Philadelphia Academy Herbarium. Information on Henry Little, its obscure collector, is scant.

1966. Thieret, J.W. Additions to the Louisiana flora. Sida 2:264-265.
[255] Ten species towards a projected Louisiana Flora.

1966. Thieret, J.W. Habit variation in *Myrica pensylvanica* and *M. cerifera*. Casta-
[256] nea 31:183-185.

Habit variation within *M. cerifera* – *M. pusilla* complex studied in Louisiana is a response to habitat and taxonomically of little significance. Specific distinction between them is untenable.

1967. Bamforth, S.S. A microbial comparison of two forest soils of southeastern
[257] Louisiana. Proc. La. Acad. Sci. 30:7-16.

A pine forest on the Prairie Terrace near Hickory (St. Tammany Parish) vs. a Delta hardwood bottomland forest south of New Orleans. Soils examined for bacteria, fungi, and protozoa. Two tables.

1967. Boudreaux, B.H. In Memorium: Percy Viosca, Jr., 1892-1961. Proc. La.
[258] Acad. Sci. 30:5-6.

See also Penn's tribute of 1962, from which much of the information here was taken.

1967. Delahoussaye, A.J. and J.W. Thieret. *Cyperus* subgenus *Kyllinga* (Cypera-
[259] ceae) in the continental United States. Sida 3:128-136.

Three of the four spp. Louisiana residents. Illustrations of achenes and spikelets, not habit; distribution maps, limited synonomy, and species descriptions. Key to subgenera or distinctive features of *Kyllinga* would have hastened our focus.

1967. [260] Duncan, W.H. Woody vines of the southeastern United States. Sida 3:1-76.

Twenty-nine genera treated, 21 occurring in the state. Physical map of study area, distribution maps, excellent drawings, keys, and species descriptions for large genera. NO and LAF material examined.

1967. [261] Ewan, J. Introduction to C.S. Rafinesque, *Florula ludoviciana* (1817). Classica Botanica Americana 5:i-xl. New York and London.

Introduction of historical and taxonomic interest and is, like Shinner's article of 1957, sympathetic to the man for whom "much maligned" has become a permanent epithet.

1967. [262] Hutto, J. and R.D. Thomas. *Hottonia inflata* (Primulaceae) in Ouachita Parish, Louisiana. Sida 3:187.

A second location for the state.

1967. [263] Pinkava, D.J. Biosystematic study of *Berlandiera* (Compositae). Brittonia 19:285-298.

B. X *betonicifolia* (Hook.) Small (pro. sp.) = *B. pumila* X *texana* to the east and west of our area, respectively. Drummond collected the type in New Orleans in 1833.

1967. [264] Radford, A.E., C.R. Bell, J.W. Hardin, and R.L. Wilbur. Contributor's guide for the "Vascular flora of the southeastern United States." Chapel Hill, North Carolina. 20 p.

A floristic manual to the forested region of the southeastern U.S., the work of some 50 contributors, was projected for publication by 1975. Individual contributions have appeared in the periodical literature while awaiting incorporation into the *Manual*. For example, *J. Elisha Mitchell Soc.* (1971 & '72) carried Hardin's "Studies of the Southeastern U.S. Flora" I, II, and III (87:39-50; 88:30-32), which provides keys, nomenclature and distribution to the Betulaceae, gymnosperms, Magnoliaceae and Illiciaceae.

1967. [265] Randolph, L.F., I.S. Nelson, and R.L. Plaisted. Negative evidence of introgression affecting the stability of Louisiana iris species. Cornell Univ., Agr. Exp. Sta., Memoir 398. 56 p.

More information is brought to bear on Anderson's treatise of introgressive hybridization (1949), with comparisons of allopatric and sympatric populations of three species and three groups of natural hybrids. See also Randolph, 1966.

1967. [266] Reese, W.D. The discovery of *Tortula vectensis* in North America. Bryologist 70:112-114.

A moss whose total known range is southern Louisiana and the Isle of Wight, England! Three figures.

1967. [267] Reese, W.D. and J.W. Thieret. Botanical study of the Five Islands of Louisiana [Iberia and St. Mary Parishes]. Castanea 31:251-277. "1966."

The "Five Islands" are Louisiana's salt domes on the central Gulf Coast, one attaining a height of more than 150 feet, and all offering habitats not otherwise afforded in the surrounding marshlands and prairie terraces. Geology, climate, phytogeography, and botanical history. Plant list includes mosses and liverworts, and bibliography includes several pertinent geological entries. Ten years later, the powers that be are at loggerheads over the use and misuse of these unique formations.

1967. [268] Thieret, J.W. Thirty additions to the Louisiana flora. Sida 3:123-127.

1967. [269] Thomas, R.D. *Burmannia biflora* (Burmanniaceae) and *Bowlesia incana* (Umbelliferae) in Ouachita Parish, Louisiana. Sida 3:183-184.

Previous state collections discussed.

1968. [270] Bamforth, S.S. Forest soil protozoa of the Florida Parishes of Louisiana. Proc. La. Acad. Sci. 31:5-15.

Seventeen forest sites examined for protozoa, algae, and proteolytic and cellulose decomposers. Forest types include oak-hickory, bottomland hardwood-cypress, and pine-deciduous. Two tables.

1968. [271] Chabreck, R.H., T. Joanen, and A.W. Palmisano. Vegetative type map of the Louisiana coastal marshes. La. Wildlife and Fish Comm. New Orleans.

Fresh, intermediate, brackish and saline marshes are recognized and plotted. See Chabreck, 1972, for full account of species composition.

1968. [272] Ewan, J. A bibliography of Louisiana botany. Southwest La. J. 7:1-83. "1967."

Reviewed by Earl L. Core, *Castanea* 33:154-155, and by F.A. Stafleu in *Taxon* 17:433-434.

1968. [273] Haynes, R.R. *Potamogeton* in Louisiana. Proc. La. Acad. Sci. 31:82-90.

Descriptions and distribution maps for each of nine species. Habit sketches from herbarium specimens are excellent; fruits also illustrated. *P. epihydrus* is new to the state's flora, known only from one locality in Washington Parish.

1968. [274] Hutchins, R.E. Island of adventure. A naturalist explores a Gulf Coast wilderness. New York. 243 p.

Island in the Pascagoula River, Mississippi. Refreshing and accurate popular account relevant to Louisiana offers much first hand, early-morning observation with the dew still on it. Botany accent is on the sublime and the curious: insectivorous and saprophytic plants, Fibonacci numbers of opposing spirals in the florets of Composite heads and the scales of pine cones, pollination tricks in jack-in-the-pulpit. Illustrated with fine black and white photographs by the author.

1968. Jones, R.E. A study of the mosses of Ouachita Parish, Louisiana. Castanea
[275] 33:18-30.

Bryological habitats discussed at length, plus annotated checklist.

1968. Kniffen, F.B. Louisiana, its land and people. Baton Rouge. 196 p.
[276]

The basic geography is more valuable than the chapters on soil and vegetation per se. Also, Spanish-moss gathering, a picturesque and nearly-vanished folk economy, pp. 98-99.

1968. Lytle, S.A. The morphological characteristics and relief relationships of
[277] representative soils in Louisiana. La. State Univ., Agr. Exp. Sta., Bull. No. 631. 23 p.

1968. Reese, W.D. New moss records for the southeastern United States. Bryolo-
[278] gist: 71:138-139.

Predominantly Louisiana collections.

1968. Reese, W.D. and R.E. Jones. *Diphyscium foliosum* in Louisiana. Bryologist
[279] 71:142.

Of phytogeographic interest, this apparent Pleistocene relict has not previously been found on the coastal plain.

1968. Richards, E.L. A monograph of the genus *Ratibida*. Rhodora 70:348-393.
[280]

R. columnifera cited from Texas and Arkansas, not Louisiana. Tulane herbarium holds an R.S. Cocks 1908 collection from R.R. tracks in Shreveport. Clair Brown (1972) calls it "widely distributed in prairie and pinelands" but must be confusing it with the common *R. peduncularis*.

1968. Robbins, H.C. The genus *Pachysandra* (Buxaceae). Sida 3:211-248.
[281]

The single American species of this southeast Asian genus is native to Louisiana, disjunct in the Tunica Hills. Voucher from West Feliciana Parish. See also item 413.

1968. Thieret, J.W. Additions to the vascular flora of Louisiana. Proc. La. Acad.
[282] Sci. 31:91-97.

As well as an annotated list of 27 new species, the accomplishments of the Louisiana Flora Project are reviewed, and mention is made of the unsatisfactory state of knowledge of the Louisiana flora.

1968. Welch, W.C. and T.E. Pope. Vines for Louisiana. La. State Univ. and Agr.
[283] and Mech. Coll., Coop. Ext. Pub. 1525. 17 p.

Pamphlet consisting mostly of a list and description of some of the native and exotic vines (44 in number) that may be grown in Louisiana, along with horticultural background. Photographs.

1969.* Anon. Weeds of the southern United States. La. State Univ. and Agr. and
[284] Mech. Coll., Coop. Ext. Pub. 1516. 42 p.

1969. Bamforth, S.S. Protozoa and algae of the Mississippi deltaic soils. Proc. La.
[285] Acad. Sci. 32:68-77.

Litters and soils from forests and grasslands of natural levee ridges, swamps, and a marsh.

1969.* Blair, R.M. and E.A. Epps, Jr. Seasonal distribution of nutrients in plants of
[286] seven browse species in Louisiana. U.S. Forest Serv., Southern Forest Exp. Sta., Res. Pap. SO-51. 35 p.

Dry matter, protein, ether extract, crude fiber, N-free extract, ash, Ca, and P contents determined. *Biol. Abst.*

1969. Depoe, C.E. *Bacopa egensis* (Poeppig) Pennell (Scrophulariaceae) in the
[287] United States. Sida 3:313-318.

First U.S. collections by Dr. Josiah Hale in the early 1800's from Louisiana remained the only collections (4 sheets at NY) apparently extant until the plant's rediscovery in the state in 1966. Summary of detective work, drawings of leaves and fruit, herbarium specimen shown. Now firmly established and here added to the state flora.

1969. Eleuterius, L.N. and S.B. Jones, Jr. A floristic and ecological study of pitcher
[288] plant bogs in south Mississippi. Rhodora 71:29-34.

Ecological brief cites fire in the maintenance of this unique subclimax community. Pitcher plant bog bibliography.

1969. Ewan, J. Historical problems for the working taxonomist. Taxon 18:194-203.
[289] A few pages on deciphering and verifying herbarium labels are illustrated by some samples from Louisiana botany: J.L. Riddell labels are examined and followed into the hands of other botanists and curators such as Joseph F. Joor, Josiah Hale, and John Torrey, with something less than fidelity to the collector's original information as one of the consequences.

1969. Ewan, J. 10 conifers for southern (New Orleans and vicinity) Louisiana. *In*
[290] Handbook on conifers. Plants and Gardens 25 (2). Special Printing, pp. 41-42.

S.L. Solymosy's "Conifers for southwestern Louisiana" appears on p. 42.

1969. Freeman, J.D. *Trillium gracile* (Liliaceae), a new sessile-flowered species
[291] from eastern Texas and Louisiana. Sida 3:289-292.

Plants previously treated as *T. ludovicianum*. Type from Texas.

1969. [292] Ingram, J. and W.J. Dress. The Louisiana irises and *Hortus Third*. Baileya 16:93-97. "1968."

The objective here is to account for Latin names used for these irises in forthcoming *Hortus Third*. *Iris* X *vinicolor* Small elucidated, and a synoptical history of the Louisiana *Iris* question becomes the fringe benefit. Three *Iris* plates reprinted from Curtis' *Botanical Magazine* and *Addisonia*.

1969. [293] Isley, D. Legumes of the United States: I. Native *Acacia*. Sida 3:365-386.

The only Louisiana *Acacia* is *A. smallii* Isely, published originally in Small's *Manual* as *Vachellia densiflora* Alexander, type from Bayou La Fourche (La Fourche Parish) near Cut-Off – a segregate of the *A. farnesiana* complex.

1969.* [294] Linnartz, N.E., *Ed.* Ecology of southern forests. La. State Univ. Proc. Ann. Forestry Symp. No. 17. 203 p.

Twelve papers discuss the relation of southern forest communities to climate, physiographic features, soil, water, and biotic factors, as well as commercial matters and modification procedures. *Biol. Abst.*

1969. [295] Miller, L.W. *Acalypha graciliens* Gray var. *delzii* L. Miller, var. nov. (Euphorbiaceae). Sida 3:447.

From Texas east into central Louisiana.

1969. [296] [Nelson, T.C. and W.M. Zillgitt]. A forest atlas of the South. U.S. Forest Serv., Southern and Southeastern Forest Exp. Sta. New Orleans and Asheville, North Carolina.

Virginia to eastern Texas, strictly maps, and these worth at least a thousand words each: soils and forest types, climate, insect pests, fire occurrence rates and more. Design and printing, the crux of such a visual book, are superb.

1969. [297] Ownbey, G. and W.A. Olson. Cytotaxonomic notes on the species of *Cirsium* native to the southeastern United States. Rhodora 71:285-296.

"*C. muticum* from Louisiana differs in small ways from the species as we are accustomed to see it in the northern wetlands." Camera lucida metaphase figures for *C. muticum* and *C. horridulum* from Louisiana collections in Lafayette Parish.

1969. [298] Reese, W.D. and A.W. Westling. *Fissidens asplenioides* on the Gulf coastal plain. Bryologist 72:71-72.

First Louisiana report of this Pleistocene relict moss.

1969. [299] Rollins, R.C. On a weed species of *Rorippa*. Rhodora 71:552-553.

R. indica (L.) Hiern. var. *apetala* (DC) Hochr., a native of eastern Asia, collected in the U.S. from Louisiana and from near Portland, Oregon.

1969. [300] Rylander, M.K. An ecological and floristic study of the vegetation of the Delta Regional Primate Research Center, Covington, St. Tammany Parish, Louisiana. Proc. La. Acad. Sci. 32:83-111.

500 acres of second growth loblolly pine forest yield 325 vascular species in ten vegetation associes. Invasion of plants in a cleared area also studied. Six figures painstakingly composed.

1969. [301] Thieret, J.W. *Baptisia lactea* (Rafinesque) Thieret, comb. nov. (Leguminosae). Sida 3:446.

Based on *Dolichos lacteus* Rafinesque, *Florula Ludoviciana*, 1817. The plant is frequent in the prairie region of Louisiana.

1969. [302] Thieret, J.W. *Dopatrium junceum* (Scrophulariaceae) in Louisiana. Sida 3:448.

1969. [303] Thieret, J.W. *Rumex obovatus* and *Rumex paraguayensis* (Polygonaceae) in Louisiana: new to North America. Sida 3:445-446.

1969. [304] Thieret, J.W. *Sagittaria guayanensis* (Alismataceae) in Louisiana: new to the United States. Sida 3:445.

Like so many of the author's discoveries, a weed in a rice field.

1969. [305] Thieret, J.W. *Trifolium vesiculosum* (Leguminosae) in Mississippi and Louisiana: new to North America. Sida 3:446-447.

1969. [306] Thieret, J.W. Twenty-five species of vascular plants new to Louisiana. Proc. La. Acad. Sci. 32:78-82.

One is the marine angiosperm *Halophila engelmannii* Aschers. *Celastrus scandens* L. (bittersweet), originally noted by R.S. Cocks in 1914 from West Feliciana, subsequently disclaimed by Clair Brown in 1945 and, following suit, by G.K. Brizicky in 1964, here readmitted to the state's flora, based on Thieret's verification of Cocks' voucher specimen at the Tulane Herbarium, evidently overlooked by Brown. Status in the wild, however, remains uncertain. (See also item 413).

1969. [307] Thieret, J.W., R.R. Haynes, and D.H. Dike. *Blyxa aubertii*e(Hydrocharitaceae) in Louisiana: new to North America. Sida 3:343-344.

Another addition to the state's noteworthy aquatic angiosperm flora, this a native of the Old World tropics.

1969. [308] Vogel, E. and A.D. Oliver, Jr. Evaluation of *Arzama densa* as an aid in the control of water-hyacinth in Louisiana. J. Econ. Entomol. 62:142-145.

The larvae of this common noctuid moth of southern Louisiana were found to feed on water-hyacinth, causing death of some plants and preventing development of seed heads on others. Pickerelweed also eaten. See *Ann. Entomol. Soc. Amer.* 62: 749-752 for life history.

1970. Anderson, L.C. Studies on *Bigelowia* (Astereae, Compositae) I. Morphology
[309] and taxonomy. Sida 3:451-465.

Two species, both Louisiana natives. State collections tabulated for morphological studies. Map and four tables.

1970. Correll, D.S., M.C. Johnston, and collaborators. Manual of the vascular
[310] plants of Texas. Renner: Texas Research Foundation. 1881 p.

Rising to the occasion of a vascular flora that numbers nearly 5000 species and embraces habitats as diverse as woodland, prairie, and desert, this is a mighty work of industry and accuracy and, for our needs, makes a fine complement to Small's 1933 *Manual* which extends west only to the Mississippi River. Louisiana is included in range citations, and discussion of the East Texas Forest Region and Gulf Prairies and Marshes Area holds true for our area as well. Species descriptions are exhaustive.

1970. Kuprionis, J. Louisiana Tech Arboretum; its history and development. Rus-
[311] ton, Louisiana. 38 p.

Includes a list of trees and shrubs in the arboretum, coded to map of same.

1970.* Meyers, S.P., M.E. Nicholson, P. Miles, J.S. Rhee, and D.G. Ahearn.
[312] Mycological studies in Barataria Bay, Louisiana, and biodegradation of oyster grass, *Spartina alterniflora*. La. State Univ., Coastal Stud. Bull. 5:111-124.

1970. Mitchell, R.S. A re-evaluation of *Polygonum meisnerianum* in North Ameri-
[313] ca. Rhodora 72:182-188.

Earliest U.S. collections seen by the author all from Louisiana: Drummond, 1832, from New Orleans; Riddell, 1838, from Madisonville (St. Tammany Parish); and Langlois, 1885 and 1892. Collections have been extremely infrequent in North America since the turn of the century, and author notes that there are no specimens at LSU or LAF.

1970. Pursell, R.A. and W.D. Reese. Phytogeographic affinities of the mosses of
[314] the Gulf Coastal Plain of the United States and Mexico. J. Hattori. Bot. Lab. 33:115-152.

The mosses of the Gulf Coast of the United States are descendents of the Tertiary moss flora of eastern North America, with a limited number of species from regions to the south.

1970. Reese, W.D. and S. Tucker. The 1967 foray of the American Bryological and
[315] Lichenological Society in Louisiana and Texas. Bryologist 73:692-701.

Collections in western Louisiana yielded 30 lichen taxa new to our state. Check list.

1970. Rense, W.C. The perique tobacco industry of St. James Parish, Louisiana: a
[316] world monopoly. Econ. Botan. 24:123-130.

A delicate and complex curing process yields high quality and flavor and high consumer demand. Circumstances beyond the control of a 300 acre per year small business make perique's future regrettably uncertain. Map and illustrations.

1970. Rhodes, D.C. *Psilotum nudum* (Psilotaceae) in North Louisiana. Sida 3:525.
[317] Lincoln Parish, extending known range 250 miles northward.

1970. Richard, M.A. The swamp maple, *Acer rubrum* var. *drummondii*, a neglect-
[318] ed native ornamental tree. La. Soc. Hort. Res. J. 11:1-23.

Gardeners may not be as interested as taxonomists and ecologists in a few of the topics, for example, morphological variability and climatic influence on date of blooming.

1970.* Smith, W.C. *Spartina* "die-back" in Louisiana marshlands. La. State Univ.,
[319] Coastal Stud. Bull. 5:89-96.

1970. Thieret, J.W. *Bacopa repens* (Scrophulariaceae) in the conterminous United
[320] States. Castanea 35:132-136.

Nomenclature; field and laboratory observations on habitat, associates, morphology; citation of U.S. collections. Thieret's field work done in the rice ponds of Acadia Parish.

1970. Thieret, J.W. *Nemophila microcalyx*, an incorrect name. Rhodora 72:399-
[321] 400.

Rafinesque again visiting nomenclatural turmoil on future generations. His epithet *trilobum* predates Nuttall's *microcalyx* and hence the correct name is *N. trilobum* (Raf.) Thieret.

1970. Thieret, J.W. Notes on *Epifagus*. Castanea 34:397-402. "1969."
[322] *E. virginiana* (Orobanchaceae). Field observations were made largely in Evangeline and East Feliciana parishes, Louisiana.

1970. Tucker, S.C. Langlois's collection sites of Louisiana lichens. Bryologist 73:
[323] 137-142.

Parish locations for about 30 sites mapped and listed, with notes and known dates of collections. A few place names cited remain unlocated: Aurelia Co. (or New Aurelia), Bayou Millien (or Millieu), Bois Charmante, and Jardin de Bouchetel. Langlois references gathered from local histories and biographical accounts.

1970. Weniger, D. Cacti of the Southwest: Texas, New Mexico, Oklahoma, Arkan-
[324] sas and Louisiana. Austin, Texas; London, England. 249 p.

The genus *Opuntia* is a minor but quite interesting floristic element in Louisiana, and this is one of our few local references. Reviewed by G.D. Rowley, *Taxon* 20:175-176; "... professional botanists are left baffled by the almost complete omission of literature citations throughout ... one looks in vain for a bibliography ..." Of more than amateur stature nonetheless.

1970. [325] Wherry, E.T. Notes on phloxes in the Gulf States. Castanea 35:198-199.

1. *Phlox philosa* subsp. *fulgida* given official status in flora of Louisiana. Earlier, unidentified Louisiana material now falls into this taxon. 2. The source of *Phlox divaricata* subsp. *lamphamii* cultivar "Opelousas," offered for sale in southwestern Louisiana, cannot be traced back to the wild in the state and remains a mystery.

1970. [326] Wright, L.D., F.J. Swaye, and J.M. Coleman. Effects of Hurricane Camille on the landscape of the Breton-Chandeleur Island chain [St. Bernard Parish] and the eastern portion of the lower Mississippi Delta. La. State Univ., Coastal Stud. Bull. 4:13-34.

Damage to marsh vegetation, pp. 26-30.

1971. [327] Bamforth, S.S. Microbial variations in the semi-tropical soils of St. Mary Parish, Louisiana. Proc. La. Acad. Sci. 33:7-12. "1970."

1971. [328] Bamforth, S.S. Floristic patterns of major groups of soil algae in Louisiana. Proc. La. Acad. Sci. 34:7-11.

Extending earlier studies (1967, '68, '69, '70) to construct a floristic pattern for the state. Synopsis of Lytle's six major soil regions of Louisiana (1968) and their characteristic vegetation. A similar study in Russia yielded comparable algal patterns.

1971. [329] Barrett, E.R. *Morchella* in Louisiana. Castanea 36:147.

M. angusticeps Pk. and *M. esculenta* (L.) Pers.

1971. [330] Choudhary, M.C. *Nitella iyengarii*, a new species from the southeastern United States. Castanea 36:209-213.

Type specimen collected by John W. Thieret from bottom of "the pool," Lacassine Wildlife Refuge, Cameron Parish.

1971. [331] Guerke, W.R. Notes on Hepaticae from Louisiana and New Mexico. Bryologist 74:202-204.

Four new state reports. Literature Cited: for "Notes on Louisiana Hepaticae" read "Southern Hepaticae" – the article contains no reference to our area.

1971. [332] Kiger, R.W. *Arthraxon hispidus* (Gramineae) in the United States: taxonomic and floristic status. Rhodora 73:39-46.

Range clarification of Louisiana supercedes Agnes Chase's 1950 revision of Hitchcock's *Manual*.

1971. Kral, R. A treatment of *Abildgaardia, Bulbostylis* and *Fimbristylis* (Cyperaceae) for North America. Sida 4:57-227.
[333]

Fifty odd tropical to warm temperate taxa, of which at least a dozen are in the state. Many chromosome counts taken from Louisiana specimens. Comprehensive monograph includes maps and fine, detailed illustrations (whole plant, spikelet, achene, leaf sheath). Field and herbarium study, LAF consulted.

1971. Leithead, H.L., L.L. Yarlett and T.N. Shiflet. 100 native forage grasses in 11 southern states. U.S. Dept. Agr., Soil Conserv. Serv., Agr. Handbook No. 389. 216 p.
[334]

For each species: description, growth characteristics, distribution, site adaptation, use and management, range map and illustrations which include ligule for identification of sterile material. Bound with glue, the leaves caducous.

1971. Nelson, B. Caroline Dormon [1888-1971]. La. Soc. Hort. Res. J. 12:42-44.
[335]

Miss Dormon's extensive knowledge of the botany and natural history of her native Louisiana had earned her a reputation as an outstanding naturalist. A world somewhat queasy with overspecialization will greatly miss her strengths.

1971.* Paden, P., P. Paden, and C.J. Felix. A study of lower and middle Cretaceous spores and pollen from the southeastern United States: II. Pollen. Pollen Spores 13(3):447-473.
[336]

Sixty-five core samples from southwestern Mississippi and northern Louisiana in which attention was devoted to the lower Tuscalossa Formation. Twenty-four genera containing 33 species described and illustrated, several of both ranks new. *Biol. Abst.*

1971. Thieret, J.W. Additions to the Louisiana flora. Castanea 36:219-222.
[337]

A further contribution to the Louisiana Flora Project begun in 1962. Eighteen new species and varieties, five of which are grasses, mostly from Thieret's own collections.

1971. Thieret, J.W. *Eriocaulon cinereum* R. Br. in Louisiana. Southwestern Nat. 15:391.
[338]

1971. Thieret, J.W. *Physalis lagascae* (Solanaceae) in Louisiana: new to the conterminous United States. Sida 4:277.
[339]

1971. Thieret, J.W. Quadrat study of a bottomland forest in St. Martin Parish, Louisiana. Castanea 36:174-181.
[340]

"Intended to augment our meager knowledge of the plant cover of the state." This Mississippi River flood plain community dominated by *Celtis laevigata*, with green ash, sweetgum, and baldcypress subordinate. Three tables.

1971. Thomas, R.D. Burmanniaceae in Louisiana. Castanea 35:329-330. "1970."
[341]

Author, curator of the herbarium at Northeast Louisiana University in Monroe, cites his collections of the three native species, all apparently rare in the state: *Apteria aphylla* (Nutt.) Barnhart, *Burmannia bifloa* L., *B. capitata* (Walt.) Mart.

1971. Thomas, R.D. Collecting vascular plants in the habitat near the ground – or,
[342] locating and collecting "Belly Plants." Castanea 36:148-149.

All author's belly-work done in Louisiana. Tiny plants may be much more common than extant herbarium specimens indicate: *Ophioglossum crotalophoroides*, previously considered rare in the state, now documented from twenty-six parishes and probably as common as bracken. Other under-two-inchers include *Lepuropetalon spathulatum* and *Tillaea aquatica*.

1972. Baker, L. and H. Beckert. A partial bibliography of the ecology and biology
[343] of the coast of the Gulf of Mexico with emphasis on the Louisiana coast. Univ. Southwest. La. Res. Ser. No. 15, Biol. 108 p.

Indexes include "Ecology," "Microorganisms," "Vegetation," "Miscellaneous," and "Bibliographies." 983 entries.

1972. Batson, W.T. A guide to the genera of native and commonly introduced ferns
[344] and seed plants of the southeastern United States, excluding peninsula Florida. Columbia, South Carolina. 151 p.

The author fails to delimit his "southeastern United States" though the cover map shows only the Atlantic coastal states. Brief descriptions and little leaf-and-flower sketches accompany each genus. Keys to families and genera.

1972. Brown, C.A. Wildflowers of Louisiana and adjoining states. Baton Rouge.
[345] 247 p.

Currently the handiest picture book on wildflower identification in our area. Thirty pages of introduction include crash courses in floral morphology, plant taxonomy, ecology, geography, and a useful color map of the parishes and vegetation regions of Louisiana. Color photographs illustrate some 400 species, including the more spectacular trees and shrubs. Inconsistent registry quality – *Spiranthes, Sisyrinchium, Pyrus*. Brief descriptions, range citations, stingy condiments. A few errors have come to my attention: *Asclepias viridiflora* Raf., p. 145, is a misinterpretation of the species illustrated. The correct name is *A. obovata* Ell. Pictures of *Liatris squarrosa* (L.) Michx. and *L. pycnostachy* Michx., pp. 210 & 211, have been transposed. And the name *Ratibida peduncularis* (T. & G.) Barnh. should probably replace *R. columnaris* (Sims) Don, a more western and northern species not elsewhere reported for Louisiana (see item 280). The picture and description agree with both. And *Salvia lyrata* is missing! Review by J. Ewan in *Quart. Rev. Biol.* 49:75-76.

1972. Chabreck, R.H. Vegetation, water and soil characteristics of the Louisiana
[346] coastal region. La. State Univ., Agr. Exp. Sta., Bull. No. 664. 72 p.

An exhaustive study with much valuable tabular information. Bibliography includes several unpublished Ph.D. dissertations of interest. Paperback, sewn in signatures, well designed and printed – an outstanding contribution in a field flooded with literature.

1972. Correll, D.S. and H.B. Correll. Aquatic and wetland plants of the southwestern United States. U.S. Environmental Protection Agency. 1777 p.
[347]

Reissued in two volumes in 1975 by Stanford University Press. Range includes the state of Texas to the Louisiana line. Thus, with Thieret's checklist of Louisiana aquatic and marsh plants (1972) as a companion, this is an invaluable contribution to the botany of our state. Full species descriptions are supplemented with full page drawings, many from other publications. The reader will find the preface to be a most eloquent – and thus controversial – plea for environmental protection.

1972. Lieux, M.H. A melissopalynological study of 54 Louisiana (U.S.A.) honeys. Rev. Palaeobot. Palynol. 13:95-124.
[348]

Pollen analyses of 54 commercial Louisiana honeys: 58 different pollen types identified. *Trifolium repens, Rubus, Berchemia scandens,* and *Salix* were high scorers. *Biol. Abst.*

1972. Lorio, P.L., Jr., V.K. Howe, and C.N. Martin. Loblolly pine rooting varies with microrelief on wet sites. Ecology 53:1134-1140.
[349]

A tree whose star is rising in the southern pinelands. Additional data towards an understanding of the dynamics of moisture stress and pine distribution. Tables & figures.

1972. Montz, G.H. A seasonal study of the vegetation on levees. Castanea 37:140-146.
[350]

East bank, St. Charles Parish. Vegetation sampled by 55 line transects at three seasons. Levees host a rich, mostly introduced, weedy flora.

1972.* Murphy, P.K. and R.E. Noble. The monthly availability and use of browse plants by deer on a bottomland hardwood area in Tensas Parish, Louisiana. Proc. Ann. Conf. Southeast. Assoc. Game and Fish Comm. 26:29-57.
[351]

1972. Newton, M.B., Jr. Atlas of Louisiana, a guide for students. La. State Univ., Misc. Publ. 72-1. 196 p.
[352]

Soils and vegetation, pp. 32-44; climate and weather; land forms.

1972. Reese, W.D. List of the mosses of Louisiana. Bryologist 75:290-298.
[353]

Based on literature reports and herbarium specimens, the moss flora of Louisiana is characterized as a diminished eastern North American flora enriched by distinct tropical American and coastal plain elements. 240 species and varieties, 90 genera, 39 families. *Fissidens neonii* is endemic to the state. Bibliography composed to complement that of Koch's 1956 paper – repetitions are minimal and the weight is on reports published later than 1956.

1972. Richard, M.A. Hardy palms for south Louisiana. La. Soc. Hort. Res. J. 13:62-83.
[354]

Thirteen palms are recommended, described and illustrated.

1972. Smith, C.A., Jr. A preliminary survey of the cultivated plants of Ouachita
[355] Parish, Louisiana. Northeast La. Univ., M.S. Thesis. Unpubl.

Representatives of 119 families, 385 genera, and 658 species and varieties were collected from cultivation or found to be on deposit at NLU. This is such an industrious contribution to a field so poorly investigated in Louisiana, that I break a general policy to include it. Needless to say, many meaningful but unpublished theses and dissertations go unnoted in this bibliography. They are often retrievable through the references cited in related, published articles.

1972. Stuckey, R.L. Taxonomy and distribution of the genus *Rorippa* (Cruciferae)
[356] in North America. Sida 4:279-430.

Five species in Louisiana. *Nasturtium micropetalum* and *N. obtusum*, types from near New Orleans, synonomous with *R. teres*. Illustrations limited.

1972. Thieret, J.W. Aquatic and marsh plants of Louisiana: a checklist. La. Soc.
[357] Hort. Res. J. 13:1-45.

Vascular plants only, with some synonomy.

1972. Thieret, J.W. Checklist of the vascular flora of Louisiana. Part I. Ferns and
[358] fern allies, gymnosperms, and monocotyledons. Lafayette Nat. Hist. Mus., Tech. Bull. 2. 48 p.

"The policy is simple: no voucher, no listing," but herbaria possessing vouchers not cited. Synonomy included. 728 species of monocots, 8 gymnosperms and 63 ferns and allies.

1972. Thieret, J.W. *Rotala indica* (Lythraceae) in Louisiana. Sida 5:45.
[359]

1972. Thieret, J.W. The yam sham. Lafayette Nat. Hist. Mus. Newsletter, March.
[360] Yams versus sweet potatoes, botanically speaking, and mention of our ornamental air-potato, *Dioscorea bulbifera*. Chatty one page mimeo.

1972. Thieret, J.W. *Zeuxine strateumatica* in Louisiana. Amer. Orchid Soc. Bull.
[361] 41:413.

An asiatic, weedy orchid that has already spread through much of Florida. Delta National Wildlife Refuge, Plaquemines Parish; new to the state.

1972. Thomas, R.D. *Botrychium lunarioides, Ophioglossum crotalophoroides,* and
[362] *Ophioglossum engelmanni* in a Louisiana cemetery. Southwestern Nat. 16: 431-432.

1972. Thomas, R.D. *Eulophia ecristata* (Fernald) Ames (Orchidaceae) in Grant
[363] Parish, Louisiana. Southwestern Nat. 16:431.

1972. [364] Wilson, B.H. and M.H. Lieux. Pollen grains in the guts of field collected tabanids in Louisiana. Ann. Entomol. Soc. Amer. 65:1264-1266.

Alluvial and salt marsh areas collected. Oak, grass, and composite pollen most abundant, the former two types windborne.

1973. [365] Allen, C.M. Additions to the Louisiana flora. Sida 5:130-131.

Four new species including *Corallorhiza odontorhiza* from St. Helena Parish. See also *Sida* 5:287 (1974) for more information on the same collection of coral-root.

1973. [366] Curry, M.G. and C.M. Allen. Alismataceae of Louisiana. Proc. La. Acad. Sci. 36:88-91.

Taxonomy of *Echinodorus* and *Sagittaria*. Key to species plus distribution maps and illustrations.

1973. [367] Feibleman, P.S. and the editors of Time-Life Books. The bayous. New York. 184 p.

Photography! And another popular book with bayou flavor is *Bayou Backwaters* by Allan W. Eckert (1968, New York, 155 p.), nature writing with strictly animal adventures: canebrake rattler vs. spotted skunk, alligator vs. armadillo.

1973. [368] Flock, J.M. Guide to the botanical contributions of Lloyd H. Shinners (1918-1971). Sida 5:137-179.

Many first reports from Louisiana by this indefatigable Texas botanist.

1973. [369] Grelen, H.E. and W.F. Mann, Jr. Distribution of *Senna seymeria (Seymeria cassioides)* – a root parasite on southern pines. Econ. Botan. 27:339-342.

The plant is an obligate parasite on at least three species of southern pines and is apparently selective for pines only. A southwide survey indicated that it is most common on moist, sandy sites of the lower Gulf and Atlantic Coastal Plains. *Punch, 1962 (1974).*

1973. [370] Guerke, W.R. Epiphyllous Hepaticae in Louisiana. Bryologist 76:201-202.

The first report of this common tropical phenomenon in Louisiana. All of the 7 species listed were collected on *Magnolia grandiflora*.

1973.* [371] Gunn, C.R. and J.V. Dennis. Tropical and temperate stranded seeds and fruits from the Gulf of Mexico. Contrib. Mar. Sci. 17:111-121.

Beaches along the western coast of Louisiana receive large numbers of tropical disseminules that have been carried by currents from the Caribbean region, northern South America, and Mexico. Disseminules of 34 tropical and 24 temperate species have been collected on northern and western Gulf beaches. *Biol. Abst.*

1973.* [372] Halls, L.K. Delicacy for the birds. La. Conserv. 25(3 & 4): 26-29.

Seed of spurges (Euphorbiaceae) is valuable for birds. Flowers of several species are pictured in color. *Punch, 1962 (1974).*

1973. Landry, G. and J.W. Thieret. *Isoëtes louisianensis* (Isoëtaceae), a new species
[373] from Louisiana. Sida 5:129-130.

Holotype from Washington Parish. The only *Isoëtes* previously collected in Louisiana is *I. melanopoda*, considered rare in the state.

1973. Lasseigne, A. Louisiana legumes. Univ. Southwest. La., Southwest. Stud.
[374] Ser., No. 1. 255 p.

Comprehensive treatment of the family in Louisiana, in which 166 species are recognized. Generic descriptions, keys to species, habitat, dates of flowering. Line drawings partially supplant species descriptions. Range maps to parish. Perfect binding, not in signatures, a misfortune. Multilithed.

1973. Mahler, W.F. By any other name. Sida 5:180-181.
[375] Louisiana botany? A Louisiana botanist, Joseph Ewan, engages Lloyd Shinners in a duel of poems: "Sat Down Be Sida" is parried by "Lines Penned in Retaliation."

1973. Montz, G.M. *Psilotum* in New Orleans. Castanea 38:207-208.
[376] *Psilotum nudum* collected on University of New Orleans (née LSU in N.O.) campus; first report from Orleans Parish. Review of previous state citations and collections. (During the 1976 AIBS meeting, several plants were discovered on Tulane campus under a row of azalea bushes.)

1973. Parks, J.C. A revision of North American and Caribbean *Melanthera* (Compositae). Rhodora 75:169-210.
[377]

M. nivea, the only U.S. species outside peninsula Florida, is a Louisiana native, and the type of *M. carpenteri* Small, a synonym, was collected in West Feliciana Parish.

1973. Pecora, R.A. A report on the algal flora of southwestern Louisiana: Phytoflagellates. Proc. La. Acad. Sci. 36:76-82.
[378]

List of 34 flagellates, of which 13 are reported for the first time in the state; annotations and more or less brief descriptions.

1973. Solymosy, S.L. *Hydrilla verticillata* (L. f.) Casp., a new plant for Louisiana.
[379] La. Soc. Hort. Res. J. 14:92.

1973. Thomas, R.D. *Dirca palustris* (Thymelaeaceae): new to Louisiana. Sida
[380] 5:132.

1973. Thomas, R.D., W.H. Wagner, Jr., and M.R. Mesler. Log fern (*Dryopteris*
[381] *celsa*) and related species in Louisiana. Castanea 38:269-274.

Update of Brown and Correll's work of 1942. Morehouse Parish.

1974. Allen, C.M. Nineteen species of grasses (Poaceae) new to Louisiana. Proc.
[382] La. Acad. Sci. 37:18-20.

Field and herbarium study.

1974. Allen, C.M. Some unusual grasses (Poaceae) of Louisiana. [Abstract.] Proc.
[383] La. Acad. Sci. 37:130.

Recently discovered hybrid: *Sphenopholis obtusata* X *S. pensylvanica*. Volumes 37 and 38 of the *Proceedings* include abstracts of papers presented at the 1974 and 1975 Annual Meetings of the Louisiana Academy. Several are here included primarily to link certain workers with certain topics.

1974. Bamforth, S.S. Coastal plankton off Grand Isle [Jefferson Parish], Louisiana.
[384] Proc. La. Acad. Sci. 37:64-69.

Collections from Freeport Sulphur Company Grand Isle Platform west of the delta. Annotated list and one figure correlating major groups with temperatures and salinity.

1974. Cain, R.H. Pimple mounds: a new viewpoint. Ecology 55:178-182.
[385] The character and distribution of pimple mounds in Louisiana and adjoining territory points to a possible pedestal tree-erosion origin. Literature cited brings out of obscurity several related publications and theses.

1974. Delcourt, H.R. and P.A. Delcourt. Primeval magnolia-holly-beech climax in
[386] Louisiana. Ecology 55:638-644.

Reconstruction of early settlement forest patterns in West Feliciana Parish from an American Land Office Survey of 1821. This study represents the first quantitative evidence to support the existence of a late-successional, or climax, magnolia-beech-holly forest in the original vegetation of upland mesic sites of the Gulf Coastal Plain. Two tables, one parish map of forest types.

1974.* Duffy, I.T. Some like it wet. Amer. Forestry 80(6):32-35.
[387] Hardwoods native to the lower Mississippi Valley generally survived the 1973 flood without serious damage. Newly planted stands as well as older trees of species not naturally found on bottomland sites, were frequently lost. *Punch, 1962 (1975).*

1974. Fruge, D.W. The vegetation of Lacassine Pool, Lacassine National Wildlife
[388] Refuge [Cameron Parish], Louisiana. U.S. Dept. Interior, Fish and Wildlife Serv., Lafayette. Mimeo.

Two major communities analyzed, emergent and floating-leaved/submergent. Checklist of 138 spp.

1974. Gonsoulin, G.J. A revision of *Styrax* (Styracaceae) in North America, Cen-
[389] tral America, and the Caribbean. Sida 5:191-258.

S. americana and *S. grandifolia* in the state, the history of the former going back to Robin's Voyages (1807). Specimens from LAF utilized.

1974. Gregory, P.E. and D.R. Sanders, Sr. Some aspects of the life history and
[390] ecology of *Cabomba caroliniana* Gray. [Abstract.] Proc. La. Acad. Sci. 37:131.

1974. Grelen, H.E. Pinehill bluestem, *Andropogon scoparius* var. *divergens* Anderss. ex Hack., an anomaly of the *A. scoparius* complex. Amer. Midl. Nat. 91:438-444.
[391]

Review of published accounts of the relation of var. *divergens* to other taxa, together with morphological investigations of transplanted clones, indicates that separation of southern forms of *A. scoparius* is taxonomically imprudent. *Punch, 1962 (1975).* More on the same appeared in *J. Range Mgmt.* 27:283-284 (1974).

1974. Jones, S.B., Jr. Mississippi Flora. 1. Monocotyledon families with aquatic or
[392] wetland species. Gulf Res. Repts. 4:357-379.

IV. Dicotyledon families with aquatic or wetland species, *ibid*, 5:7-22 (1975). Keys, distribution maps (in Miss.), habitats, references, nomenclature, and notes are given for some 28 families (grasses, sedges, rushes excluded) many of whose members spill over into Louisiana.

1974.* Kapraun, D.F. Seasonal periodicity and spatial distribution of benthic marine
[393] algae in Louisiana. Contrib. Mar. Sci. 18:139-167.

A broad investigation providing information on physiology, taxonomy, floristic affinities, and life histories. A list of 85 benthic marine algae including 31 new records for Louisiana is given. *Biol. Abst.*

1974. Luke, W.J., C.A. Schexnayder, and C.A. Brown. Establishment of *Tillandsia recurvata* L. in East Baton Rouge Parish, Louisiana. Proc. La. Acad. Sci. 37:17.
[394]

Seconding Thieret's provisional inclusion of ball-moss (1969) in the state flora based on a 1939 Viosca collection from parts unknown. The plant is established on an ornamental yaupon on the LSU campus, and the groundskeeper has agreed to go easy.

1974. Montz, G.M. *Linaria vulgaris* Hill in Louisiana. Castanea 39:190.
[395]

1974. Montz, G.M., and A. Cherubini. An ecological study of a bald-cypress
[396] swamp in St. Charles Parish, Louisiana. Castanea 38:378-386. "1973."

Quadrat sampling: DBH and frequency-density of cypress. Of particular interest are a comparison of township maps of 1860 to quadrangle maps of 1969 in study of plant succession, documenting baldcypress' extension into adjacent marsh, and discussion of a change from lower to higher salinities in the Mississippi River-Gulf outlet area and Lake Pontchartrain, to the detriment of baldcypress and doubtless many other plants.

1974. [397] Oefinger, S.W., Jr. and L.K. Halls. Identifying woody plants valuable to wildlife in southern forests. U.S. Forest Serv., Southern Forest Exp. Sta., Res. Pap. SO-92. 76 p.

Twigs, buds, and other key identification features are illustrated in color for 70 browse species common to pine-hardwood forests of the South. *Punch, 1962 (1975).*

1974. [398] Pecora, R.A. Reports on the algal flora of southwestern Louisiana. II. Collections of Chlorophyceae and Xanthophyceae. Proc. La. Acad. Sci. 37:50-54.

Eighteen of the 19 species reported for the first time in the state.

1974. [399] Piehl, M.A. Preliminary reports on the flora of Louisiana. No. 1. The families Magnoliaceae, Illiciaceae, and Schisandraceae. [Abstract.] Proc. La. Acad. Sci. 37:131.

1974. [400] Piehl, M.A. Rare or endangered higher plants of Louisiana – a progress report. [Abstract.] Proc. La. Acad. Sci. 37:131.

Comprehensive state list has been prepared.

1974. [401] Piehl, M.A. Verification of the occurrence of *Tillandsia recurvata*, ball-moss, in Louisiana and its endangered status. La. Soc. Hort. Res. J. 15:1-6.

Locally abundant on L.S.U. campus! See item 394.

1974. [402] Piehl, M.A. and M.A. Spindler. Preliminary reports on the flora of Louisiana. No. 4. The family Lauraceae. [Abstract.] Proc. La. Acad. Sci. 37:131.

Range of *Lindera benzoin* (L.) Bl. considerably wider than an early report by Cocks suggests.

1974. [403] Piehl, M.A. and P.A. Piehl. Preliminary reports on the flora of Louisiana. No. 2. The families Aristolochiaceae, Celastraceae, and Menispermaceae. [Abstract.] Proc. La. Acad. Sci. 37:131.

1974. [404] Piehl, P.A. and M.A. Piehl. Vines of Louisiana, part I. Louisiana lianas, a provisional annotated list of native, naturalized and cultivated woody vines. La. Soc. Hort. Res. J. 15:51-60.

35 families, 60 genera and 128 species.

1974. [405] Reese, W.D. Noteworthy Louisiana mosses. [Abstract.] Proc. La. Acad. Sci. 37:131.

1974. Sanders, D.R., Sr. Notes on the appearance of a new aquatic plant in
[406] Louisiana. [Abstract.] Proc. La. Acad. Sci. 37:132.

Hydrilla verticillata Royle, potentially a dangerous introduction into Louisiana waters. Solymosy, however, reported it in 1973.

1974. Sanders, D.R., Sr. and J.H. Mannings. Effects of water fluctuation on the
[407] vegetation of Black Lake. [Abstract.] Proc. La. Acad. Sci. 37:132.

Effective and, according to authors, ecologically sound method of removing unwanted aquatic plants.

1974. Short, M.S. and M.A. Piehl. Preliminary reports on the flora of Louisiana.
[408] No. 3. The family Annonaceae. [Abstract.] Proc. La. Acad. Sci. 37:132.

1974. Spindler, M.A. and R.E. Noble. Fall vegetation on the spoil banks of Superi-
[409] or Canal, Cameron Parish, Louisiana. Proc. La. Acad. Sci. 37:74-88.

An artificial community that is increasing in a state where a six inch change in elevation can significantly alter the plant life.

1974. Thieret, J.W. and C.M. Allen. *Setaria pallide-fusca* (Gramineae) in Louisi-
[410] ana. Castanea 39:290-291.

This LSU campus weed proves new to state, to conterminous U.S. and to North America.

1974. Valentine, J.M., Jr. Unpublished administrative reports. U.S. Dept. Interi-
[411] or, Fish and Wildlife Serv., Lafayette. 5 p. Mimeo.

Titles from 1960 to 1974, mostly grazing and succession studies in local wildlife refuges. No authors.

1975. Allen, C.M. *Trichomanes petersii* in Louisiana. [Abstract.] Proc. La. Acad.
[412] Sci. 38:121.

1975. Delcourt, H.R. and P.A. Delcourt. The blufflands: Pleistocene pathway into
[413] the Tunica Hills [West Feliciana Parish]. Amer. Midl. Nat. 94:385-400.

Numerous plant species of a northern mixed mesic forest reach their southern terminus in the hilly land above the eastern escarpment of the Mississippi River alluvial valley known as the Tunica Hills. The epic of several of these Pleistocene migrants and relicts is here explored in full.

1975. Duncan, W.H. and L.E. Foote. Wildflowers of the southeastern United
[414] States. Athens, Georgia. 296 p.

In his foreword, ex-governor of Georgia, Jimmy Carter, praises this reference as "both comprehensive and beautiful." Indeed it expands the concept of a popular wildflower book by its conviction that even the amateur botanist deserves the most accurate and thorough botany. Range includes Louisiana. Illustrated with color photographs. Reviewed by Earl L. Core, *Castanea* 40:364 (1975) and by J. Ewan, *Ecology* 58:222-223 (1977).

1975. Elliott, P.B. and S.S. Bamforth. Interstitial protozoa and algae of Louisiana
[415] salt marshes. J. Protozool. 22:514-519.

Sediments of stagnant pools among *Spartina* sp. and *Distichlis spicata* constitute a "sulfide biome" in which the abundance of nutrients provides habitable conditions for all the major groups of microflora. Excellent figures.

1975. Gould, E. and J. Ewan. Phytogeographic and ecologic relationships of the
[416] flora of Breton Island [St. Bernard Parish], Louisiana. Tulane Stud. Zool. Botan. 19:26-36.

Island 3 miles long by ½ mile wide. Salt spray community of 84 species of vascular plants and 3 mosses, predominantly of temperate origin, studied in light of records published 60 years previously.

1975. Graham, S.A. Taxonomy of the Lythraceae in the southeastern United
[417] States. Sida 6:80-103.

Cuphea glutinosa "first collected in the United States in 1884 in Vermilion Parish, Louisiana." Chromosome count based on Thieret collection from Lafayette Parish. Further information on *Rotala indica* (see Thieret, 1972). All seven genera treated are in our state. Material from LAF consulted. Illustrations and maps wanting.

1975. Guerke, W.R. A floristic study of the Hepaticae and Anthocerotae of the
[418] Florida Parishes. Bryologist 77:593-600.

Physical description and vegetation of the study area, floristic comparisons and phytogeography, as well as a list of 83 species in 24 families.

1975.* Johnson, R.L. Natural regeneration and development of Nuttall oak and
[419] associated species. U.S. Forest Serv., Southern Forest Exp. Sta., Res. Pap. SO-104. 12 p.

Nuttall oaks from a dense seedling catch survived for 5 to 10 years in complete shade and for 15 years with 1 or 2 hours of daily sunlight. They made little growth, but they responded well when released after periods of 1 to 9 years. Green ash, water hickory, and sugarberry survived equally well and outgrew the oaks after the overstory was removed. *Punch, 1962 (1975).*

1975. Johnston, L.A. Revision of the *Rhamnus serrata* complex. Sida: 6:67-79.
[420] Louisiana un-botany: *R. lanceolata* "is unknown in Louisiana" though collections are mapped from neighboring east Texas.

1975. Jones, R.E. Louisiana Tech University Herbarium: new national plant depository for U.S. Corps of Engineers. [Abstract.] Proc. La. Acad. Sci. 38:121.
[421]

Louisiana Tech chosen as the voucher specimen depository for Corps of Engineers' new Environmental Effects Laboratory Waterways Experiment Station, Vicksburg, Mississippi.

1975. Landry, G.P. Unusual pteridophytes of Louisiana. [Abstract.] Proc. La. Acad. Sci. 38:121.
[422]

1975. Lieux, M.H. Dominant pollen types recovered from commercial Louisiana honeys. Econ. Botan. 29:87-96.
[423]

Same honey samples as Lieux, 1972, and some of the same information. Additionally, electron micrographs and morphological descriptions of pollen grains. Two maps.

1975. Marx, P.S. and R.D. Thomas. A survey of the vascular plants of Caldwell Parish, Louisiana. Proc. La. Acad. Sci. 38:75-85.
[424]

924 species. Area near Horseshoe Lake north of Columbia is the only Louisiana site for *Dirca palustris* (see Thomas, 1973). Two others new to the state: *Quercus oglethorpensis* and *Zanthoxylum americanum*.

1975. Massey, J.R. *Fatoua villosa* (Moraceae): additional notes on distribution in the southeastern United States. Sida 6:116.
[425]

See also, Thieret, 1964.

1975. Montz, G.N. The submerged vegetation of Lake Pontchartrain, Louisiana. U.S. Army Corps of Engineers, New Orleans District, Environ. Qual. Sect. 17 p. Mimeo.
[426]

Vallisneria americana, *Ruppia maritima*, and *Najas guadalupensis* most abundant. Distribution maps.

1975. Noble, R.E. and P.K. Murphy. Short term effects of prolonged backwater flooding on understory vegetation. Castanea 40:228-238.
[427]

Mississippi River bottomland hardwood forest in Tensas Parish sampled before and after flood. Elimination of six taxa, in contrast to the vegetation's general resilience, carries implications on range and tolerance of species in an unstable environment.

1975. Pecora, R.A. Rediscovery of *Oscillatoria ludoviciana* Flint and Prescott. [Abstract.] Proc. La. Acad. Sci. 38:121.
[428]

1975.* Sand, N.H. and P. Koch. Creole carpentry in 1800. Forests and People 25(3):16-19, 38-45.
[429]

The Kent Plantation House, in Alexandria (Rapides Parish), Louisiana, exemplifies construction practices in which reliance was almost exclusively on local materials. Though French tradition and culture predominated in Louisiana, carpenter's tools of English design seem to have been preferred. *Punch, 1962 (1976)*. See also where La. compared with St. Louis in scholarly paper by Charles E. Paterson, "Houses of French St. Louis," in J.F. McDermott, *French in Mississippi Valley*, 1965, 17-40, illus.

1975. Somers, P. and W.R. Buck. *Selaginella ludoviciana, S. apoda* and their
[430] hybrids in the southeastern United States. Amer. Fern J. 65:76-82.

Hybrids are rare but have been reported for Florida and Louisiana.

1975. Sullivan, V.I. Wind pollination in *Eupatorium* (Compositae). [Abstract.]
[431] Proc. La. Acad. Sci. 38:121-122.

1975. Thieret, J.W. *Hemigraphis reptans* (Acanthaceae), a greenhouse weed in
[432] Louisiana. Sida 6:115.

1975. Thomas, R.D. and R. Overby. A preliminary survey of the vascular flora of
[433] Caddo Parish, Louisiana. [Abstract.] Proc. La. Acad. Sci. 38:122.

INDEX TO AUTHORS

Perdue, Robert E., Jr. 1962
Pessin, Louis J. 1928
Phaff, Herman J. 1952
Piehl, Martin A. 1974
Piehl, Paula A. 1974
Pinkava, Donald J. 1967
Plaisted, Robert L. 1967
Plakidas, Antonios G. 1956, 1960
Pope, Thomas E. 1968
Prescott, Gerald W. 1942
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Pursell, Ronald A. 1956, 1958, 1970
Putnam, John A. 1956
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A SEASONAL AND ECOLOGICAL SURVEY OF FRESHWATER LIMPET SNAILS (PULMONATA: ANCYLIDAE) AND THEIR DIGENETIC TREMATODE PARASITES IN SOUTHEASTERN LOUISIANA

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ABSTRACT

An 18-month survey involving almost 20,000 freshwater limpet snails of the family Ancylidae revealed three species, each representing a different genus, occurring in southeastern Louisiana.

Laevapex fuscus was collected only from lentic habitats, where it exhibited, at most, a bivoltine pattern of reproduction with two successive generations per year; in habitats of low primary productivity a single annual generation was produced. *Ferrissia fragilis* was collected from lotic and lentic habitats and produced a single annual generation. *Hebetancylus excentricus* also displayed a broad habitat preference but exhibited up to a trivoltine pattern of reproduction.

Southeastern Louisiana ancylid snails play a major role in the ecology of digenetic trematodes since 19 species of larval trematodes were found developing in three ancylid species. Hosts, descriptions, seasonal incidence, and possible identity of these cercariae are given.

Seasonal occurrence of trematode intramolluscan stages was closely related to seasonal occurrence of the ancylid snail hosts. Bivoltine patterns of reproduction for *Hebetancylus excentricus* were reflected in two generations of cercarial production.

On the basis of comparative ecology, anatomy, and hosted trematodes, we propose that *Hebetancylus* occupies an intermediate phylogenetic position between *Ferrisia* and *Laevapex*. *Ferrissia* is least specialized in terms of its hosted trematode fauna, which bears similarity to that hosted by snails of the family Planorbidae.

INTRODUCTION

Literature on parasites of ancylid snails is meager, with less being known than for other major families of freshwater gastropods (Malek and Cheng, 1974). Smith (1967) reviewed the literature on larval digenetic trematodes developing in ancylids and noted that the six reports from 1827 to 1959 were incomplete in description, with no indication as to specific or generic identity of the adult trematodes. None was from North America.

Smith (1959) was the first to report North American ancylid snails as first intermediate hosts for trematodes. He reported the occurrence of *Megalodiscus temperatus* (Stafford, 1905) in *Ferrissia fragilis* (Tryon, 1863) in Michigan. The life cycle of this rectal parasite of frogs had been elucidated by Krull and Price (1932), who implicated the planorbid snail *Helisoma trivolvis* (Say, 1817) as a natural snail host.

Peters and Self (1963) reported an ophthalmoxiphidiocercaria of the family Allocreadiidae Stossich, 1903 developing in *Laevapex fuscus* (C.B. Adams, 1841) from southeastern Oklahoma and encysting in the mantle of unionid clams and limpets, including limpets hosting the rediae. These investigators believed the cercaria to be that of *Allocreadium ictaluri*

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Pearse, 1924, an intestinal parasite of catfish. They noted that miracidia, hatched from eggs obtained from infected catfish, penetrated and remained in the tissues of *L. fuscus*. All other members of the trematode family Allocreadiidae, for which life cycles are known, utilize sphaeriid clams as first intermediate hosts (Yamaguti, 1975).

Basch (1963), in his monograph on North American Ancylidae, noted that of 150 ancylid collections taken during the summer of 1961, from 23 states, about 15% were heavily infected with one or more species of trematode larvae.

Smith (1967) examined *Ferrissia fragilis, F. parallela* (Haldeman, 1841), and *Laevapex fuscus* from several marsh pond, stream, and river localities in southeastern Michigan. Fifteen different trematode species were found to use one or more of the three limpet species as first intermediate hosts. Unfortunately, Smith did not figure or otherwise describe those cercariae except to note that *Megalodiscus temperatus* developed in all three limpet species. Identification of the other 14 cercariae was only to the level of superfamily or family.

In addition to *Megalodiscus temperatus*, Smith (1967) noted another amphistome developing in *Ferrissia parallela*; a strigeoid in *F. fragilis*; another in *F. parallela*; an echinostomatid in *F. fragilis*; two others in *F. parallela*; a fourth in *Laevapex fuscus*; a spirorchiid in *F. fragilis, F. parallela,* and *L. fuscus*; a lissorchiid and cyanthocotylid in *L. fuscus*; and three xiphidiocercariae in *F. parallela*. Significance of the apparent specificity exhibited by most cercariae is tempered by Smith's failure to note the occurrence of sympatry among the limpet hosts.

Smith (1968) reported that lissorchiid cercariaea (tailless cercariae), previously reported (Smith, 1967) in *Laevapex fuscus* from Michigan, also parasitized *Ferrissia rivularis* (Say, 1817) in southeastern Michigan. According to Smith, this cercariaeum was identical to *Cercariaeum mutabile* described by Cort (1918) and reported by Wallace (1941) to be the larva of *Triganodistomum mutabile* (Cort, 1918), an intestinal parasite of catostomid fishes. Wallace (1941) reported *Helisoma trivolvis* and *H. campanulata* (Say, 1821) as natural snail hosts, with the planarian *Dugesia* sp. or the commensal annelid, *Chaetogaster limnaei* von Baer, 1827 serving as second intermediate host for *T. mutabile*.

Duncan and DeGiusti (1976) produced evidence that the lisorchiid cercariaeum, thought by Smith (1968) to be *Cercariaeum mutabile*, was in fact a complex of three cercarial species. These cercariaea differed in size, arrangement of tegumental papillae, tegumental spination patterns, and species of intermediate hosts. Since Duncan and DeGiusti believed them to be larval stages of described lissorchiids, they did not formally describe them as new species. They did, however, provide full descriptions while designating them as *Cercariaeum* types I through III. *Cercariaeum* type I utilized *Laevapex fuscus* as first intermediate host with *Chaetogaster limnaei* as second intermediate. *Cercariaeum* types II and III utilized *L. fuscus* and *Ferrissia rivularis* respectively, while *Chaetogaster limnaei, Dugesia tigrina* (Girard, 1850) and *D. dorotocephala* (Woodworth, 1897) served as second intermediates.

Underwood and Dronen (1977) reported an unidentified species of *Ferrissia* from Texas as an experimental host for the frog lung fluke *Haematoloechus breviplexus* Stafford, 1902. These investigators noted that xiphidiocercariae obtained from *Ferrissia* sp. were smaller at maturity than *H. breviplexus* cercariae described by Schell (1965) from the experimentally infected planorbid snail *Gyraulus similaris* (F.C. Baker, 1919).

Turner and Corkum (1977) reported *Ferrissia fragilis* as a natural snail host for the turtle blood fluke *Spirorchis scripta* Stunkard, 1923 in Louisiana. The larva of *S. scripta* had previously been reported to develop in certain species of naturally infected planorbid snails (Goodchild and Kirk, 1960; Holliman and Fisher, 1968). From the above review, ancylids obviously appear to have been a neglected group in most parasitological studies.

The objectives of this study were as follows: (1) to survey the freshwater limpet (Ancylidae) fauna of southeastern Louisiana, (2) to investigate related ecological aspects including habitat, seasonality, and population dynamics, (3) to investigate its role in the ecology of digenetic trematode parasites, (4) to provide descriptions and figures of those trematode cercariae developing in southeastern Louisiana ancylids, (5) to identify cercariae by life cycle studies and/or a survey of trematode life history literature, and (6) to postulate a phylogenetic relationship for southeastern Louisiana ancylids based upon similarities and differences in hosted trematodes.

MATERIALS AND METHODS

Limpets were collected biweekly, for up to 18 consecutive months, from five ecologically dissimilar localities in southeastern Louisiana. Collecting sites, with survey period in parentheses, were as follows: drainage ditch on Ben Hur Road Experimental Farm, 1 mi S of LSU Baton Rouge campus, East Baton Rouge Parish, (June 1975-November 1976); Beaver Pond Branch, 3 mi SE of Livingston, Livingston Parish. on Interstate Highway 12 (July 1975-November 1976); borrow pit on W side of Atchafalaya floodway levee at Ramah, Iberville Parish, on Interstate Highway 10 (July 1975-August 1976); roadside swamp, 2 mi SE of Sorrento, Ascension Parish, on Rt. 61 (June 1975-July 1976); and pond, 2 mi E of Head of Island, Livingston Parish, on Rt. 22 (June 1975-August 1976).

Collections were made by removing, with a sharp scalpel blade, limpets attached to submerged or floating debris as well as leaves and stems of floating or submerged vegetation. Specimens were placed in glass finger bowls containing water from the collecting site. Bowls rested on an inverted styrofoam ice chest that served as a floating work table.

Collecting time for each of the 156 collections was a multiple of 15 minutes duration. This was done to establish an index of relative abundance by noting number of limpets collected during 15 minutes. To roughly determine population structure, all individuals seen, regardless of size, were collected.

Snails were maintained in their collection containers until identified, graded into sizes, and examined for larval digenetic trematodes; this was usually done within 24 hours after collection. Voucher specimens of all limpet species were deposited in the mollusc collection of the Delaware Museum of Natural History (DMNH).

The smaller limpet species *Ferrissia fragilis* (DMNH 119530) was graded into three size classes based upon shell length: <2 mm, 2-4 mm, and>4 mm. *Laevapex fuscus* (DMNH 119532) and *Hebetancylus excentricus* (Morelet, 1851) (DMNH 119531) were graded into classes:<3 mm, 3-5 mm, and>5 mm. Presumably changes, over the course of our survey, in relative numbers of each class should reflect population dynamics, including reproduction, recruitment, and death. Although collections were biweekly, data on limpet populations were pooled for each month.

Visual screening for digenetic trematode larvae was possible since most of the limpet's "soft-parts," including the digestive gland, were exposed to inspection when the snail was inverted. Identification was made by dissection or by allowing cercariae to emerge from live, isolated individuals. Limpets without visible germinal sacs (rediae or sporocysts) were dissected and examined for immature larval stages and/or metacercariae.

Biweekly data on incidence of infection, like those used for population biology, were pooled for each month. Only those individuals of *Hebetancylus excentricus* and *Laevapex fuscus* greater than 3 mm shell length were considered when computing monthly incidence. Neither cercariae or germinal sacs were evident among the smaller individuals; however, this was not true for *Ferrissia fragilis*, all sizes of which were considered when computing incidence.

Cercariae, designated as types I-XIX (Figures 1-19) were studied live and unstained, vitally stained with nile blue, or fixed in hot 10% formalin. Unless otherwise noted, measurements were taken from 10-20 formalin preserved specimens under light coverslip pressure and are expressed in microns. Ranges are given with mean in parentheses. Drawings are composites made from live and preserved specimens, either free hand, with aid of a microprojector, or from photomicrographs.

RESULTS AND OBSERVATIONS

Ecology of Southeastern Louisiana Ancylids

After 18 months of collecting and examining almost 20,000 ancylid specimens, three species, each representing a different genus, were found to occur in our study areas. *Laevapex fuscus* was collected from submersed stems of emergent vegetation and from submersed debris at three localities exhibiting a lentic character. *Ferrissia fragilis* and *Hebetancylus excentricus* occurred on emergent and floating vegetation at all five collecting sites, which along with the seasonality and population dynamics of their ancylid snail faunas, are characterized below.

1. Ben Hur Experimental Farm (BHF)

This 3 m wide, mud-bottom ditch, although never dry, had an intermittent flow and drained the LSU experimental farm and 20 shallow ponds for experimental rearing of catfish and crayfish. During the 18-month survey of this locality, 3,774 *Hebetancylus excentricus* and 172 *Ferrissia fragilis* were collected exclusively off submersed leaves and stems of alligator weed (*Alternanthera* sp.). *Laevapex fuscus* was not seen or collected.

Population dynamics and seasonal abundance of both *Ferrissia fragilis* and *Hebetancylus excentricus* are presented in Figure 20. *F. fragilis* was collected intermittently and in small numbers during the course of the survey at BHF. Usually fewer than two individuals were collected per 15 minutes of collecting effort. A peak in numbers occurred in April, when about 10 limpets were collected per 15 minutes. This peak was followed by a gradual decline to zero in August. Recruitment occurred in mid spring as evident by the increasingly greater percentage of the population comprised by individuals of the small size class (<2 mm length). Individuals of the large size class (>4 mm length), probably representing the post-ovigerous segment of the population, were collected only at this time. Basch's (1963) observation of maximum length of 4 mm for *F. fragilis* may substantiate a post-ovigerous role for those large size class individuals. However, large size class (>5 mm length) *Laevapex fuscus* and *H. excentricus*, noted by Basch to have maximum lengths of 7.75 and 5.8 mm respectively, would not necessarily comprise the post-ovigerous segment.

Hebetancylus excentricus was present throughout the study and exhibited two distinct population peaks: one in November, and another in May. This species displayed a bivoltine pattern of reproduction with two successive generations per year as evident by the observation that peaks in the index of relative abundance coincide with or closely follow periods of increase in percentage of small size class individuals (< 3 mm length). In *H. excentricus*, reproduction and recruitment are preceded by a build up in percentage of the large size class sector of the population.

2. Beaver Pond Branch (BPB)

This narrow, continuously flowing stream originates near Livingston, Louisiana, and empties into Hog Branch, a larger, sand-bottomed stream forming part of the drainage for the so-called Florida Parishes of southeastern Louisiana. During periods of high water in Hog Branch (two occurred during our survey) BPB received backwater from Hog Branch. This condition persisted for several days before normal flow returned in both streams.

Hebetancylus excentricus and *Ferrissia fragilis* were collected from floating vegetation and from emergent arrowhead (*Sagittaria* sp.). *Laevapex fuscus* was not encountered. Figure 21 shows population biology and seasonal abundance of 1,294 *H. excentricus* and 1,853 *F. fragilis* collected during 17 months. Seasonality is evident and perhaps reflects seasonal partitioning of the habitat by the two limpet species. From January to July, 1976, *F. fragilis* was present in large numbers at a time when *H. excentricus* was almost absent from the habitat. *H. excentricus* became the predominant limpet species during the fall.

3. Ramah (RAM)

This site is a borrow pit of the Atchafalaya River Basin and is subjected to large fluctuations in water level. Because of fluctuations, emergent vegetation that consisted mainly of *Sagittaria* was seasonal, and occurred mostly in summer and fall. Although no measurement of dissolved oxygen was taken during the study, this habitat would be classified as mesotrophic.

All three limpet species were sympatric at RAM. *Laevapex fuscus* was collected from submersed and floating debris, water hyacinth (*Eichornia crassipes*), and emergent *Sagittaria*. *Ferrissia fragilis* and *Hebetancylus excentricus* were similarly collected; however, *H. excentricus* was seldom found on debris. Limpet population biology and seasonal abundance for 3,663 *L. fuscus*, 577 *F. fragilis*, and 425 *H. excentricus* collected during our 14-month survey are presented in Figure 22.

As at BPB, *Hebetancylus excentricus* and *Ferrissia fragilis* displayed a pronounced seasonality that was interpreted as seasonal partitioning of the habitat. However, seasonality of limpets may also reflect seasonal absence of vegetation on which *H. excentricus* was most often collected. *F. fragilis*, like the BPB population, was abundant in early spring through summer, while *H. excentricus* was most abundant during the fall. Data indicate production of a single *H. excentricus* and *F. fragilis* generation per year.

Laevapex fuscus was the predominant limpet species at RAM and was collected in relatively high numbers almost year round. The low fall-winter index of relative abundance may have been due to *L. fuscus* burrowing into the mud, where they were unavailable for collection by our methods. Indications are that a single generation is produced annually. Recruitment certainly began in April, because population structure for that month demonstrates an expanding population.

4. Sorrento (SOR)

This is a shallow, former, roadside swamp, with a mud bottom. Water level was maintained at about 0.5 m during the first 12 months of the survey; however, in June 1976 the level began to drop and the site was completely dry by August 1976. The 100 m X 30 m area had been cleared several years earlier as right of way for an underground pipeline, and was free of trees. As a result, a luxuriant growth of emergent grass (*Paspalum* sp.) was maintained almost year round and gave the locality a marsh appearance. This site, with its shallowness, abundant emergent vegetation, and high primary productivity, fits the criteria of a eutrophic habitat.

All three ancylid species occurred at this locality; however, as seen in Figure 23 the scale for relative abundance of *Laevapex fuscus* is 10 fold greater than for *Hebetancylus excentricus* and 100 fold greater than for *Ferrissia fragilis*. Total numbers collected were 4,960, 352, and 40, respectively.

Ferrissia fragilis was collected in too small numbers for any determination of population dynamics; however, a pronounced seasonality was noted. *Hebetancylus excentricus* appears to have a single generation each year with recruitment in the spring.

Laevapex fuscus produced a fall and spring generation. Egg hatching and recruitment from one biannual cycle extended into the next, and thus gave the appearance of year-round reproduction. Another observation concerning the *L.*

fuscus population was the predominance of large-size class individuals in most pooled monthly samples. Predominance of large individuals indicates a rapid growth rate, probably attributable to the eutrophic environment, and is striking when compared to the pooled monthly population structures at the less eutrophic Ramah (Figure 22). As will be shown later, apparent differences in productivity have considerable implications for the ecology of the respective digenetic trematode populations.

5. Head of Island Pond (HIP)

This permanent pond has a shallow margin at its north end lined with emergent vegetation. The remaining margin was deep and without emergent vegetation. Much sunken debris – sheets of plastic, metal cans, glass, etc., was found along the front or south margin. *Laevapex fuscus* occurred on this debris; however, because of depth, collecting was difficult. For this reason, *L. fuscus* was not included among the ancylids studied at this locality. We mention the occurrence because it demonstrates habitat selection by the three ancylid species, since *L. fuscus* was found only on this deep water debris, while *Hebetancylus excentricus* and *Ferrissia fragilis* occurred only on debris and emergent vegetation along the shallow margin.

Population biology and seasonal abundance for 1,836 *Hebetancylus excentricus* and 182 *Ferrissia fragilis* collected during our 15-month survey are shown in Figure 24. *F. fragilis* was abundant only in February and March. We believe that presence of individuals classed as large, accompanied by an increasing percentage of the smaller class, indicates recruitment at this time.

Hebetancylus excentricus occurred year round with production of three generations; one in the summer, another in the fall, and the third in the spring.

Digenetic Trematodes in Southeastern Louisiana Ancylids

Cercariae representing 19 trematode species were found developing in one or more of three ancylid species. Hosts, descriptions, seasonality of incidence, and possible identity of these larvae are given below (Figures 20-24).

Cercaria Type I (Figures 1, 21, 22, and 23)

Laevapex fuscus collected from SOR, *Ferrissia fragilis* from BPB, and both species from RAM were found to harbor infections with xiphidiocercariae of the *armatae* group and designated *Cercaria* type I.

Description: Body 228-276(254) long by 84-112(99) wide and covered with small spines that become less dense at the posterior end. Caudal pocket present. Tail 184-228(205) long by 29-35(32) wide at base. Oral sucker 53-63(58) long by 56-64(61) wide. Acetabulum 45-51(47) long by 44-53(50) wide. Stylet shouldered, 28-33(31) long. Five pairs of pre-acetabular penetration glands with ducts that empty near stylet. Ceca extend to post-acetabular level. Excretory bladder cellular and Y-shaped. Flame cell formula or number not determined.

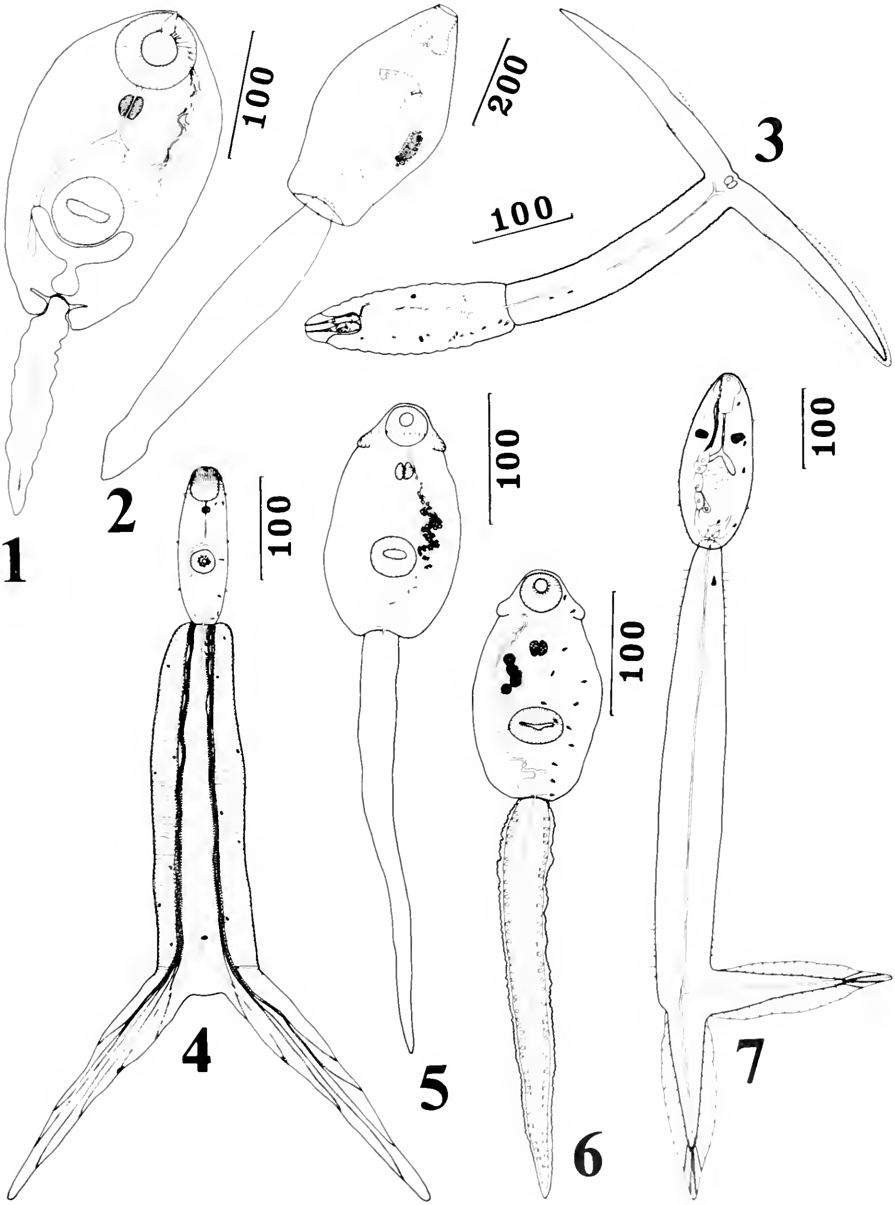
Ferrissia fragilis harboring these cercariae were collected only during July of the second summer and comprised 1% of the sampled population at BPB (Figure 21). Infection occurred in 0.8% of the sampled *F. fragilis* population during the same month at RAM (Figure 22). *Laevapex fuscus* from this locality, however, harbored infection throughout spring and summer. At SOR (Figure 23) *Cercaria* type I was present in *L. fuscus* almost year round with a peak seasonal incidence of 8.5% in August.

Cercaria Type II (Figures 2, 20, 21, 23, and 24)

Amphistome cercariae of the *diplocotylea* type, designated *Cercaria* type II, were found developing in both *Laevapex fuscus* and *Ferrissia fragilis* collected at SOR. *F. fragilis* from BHF, HIP, and BPB also harbored infections.

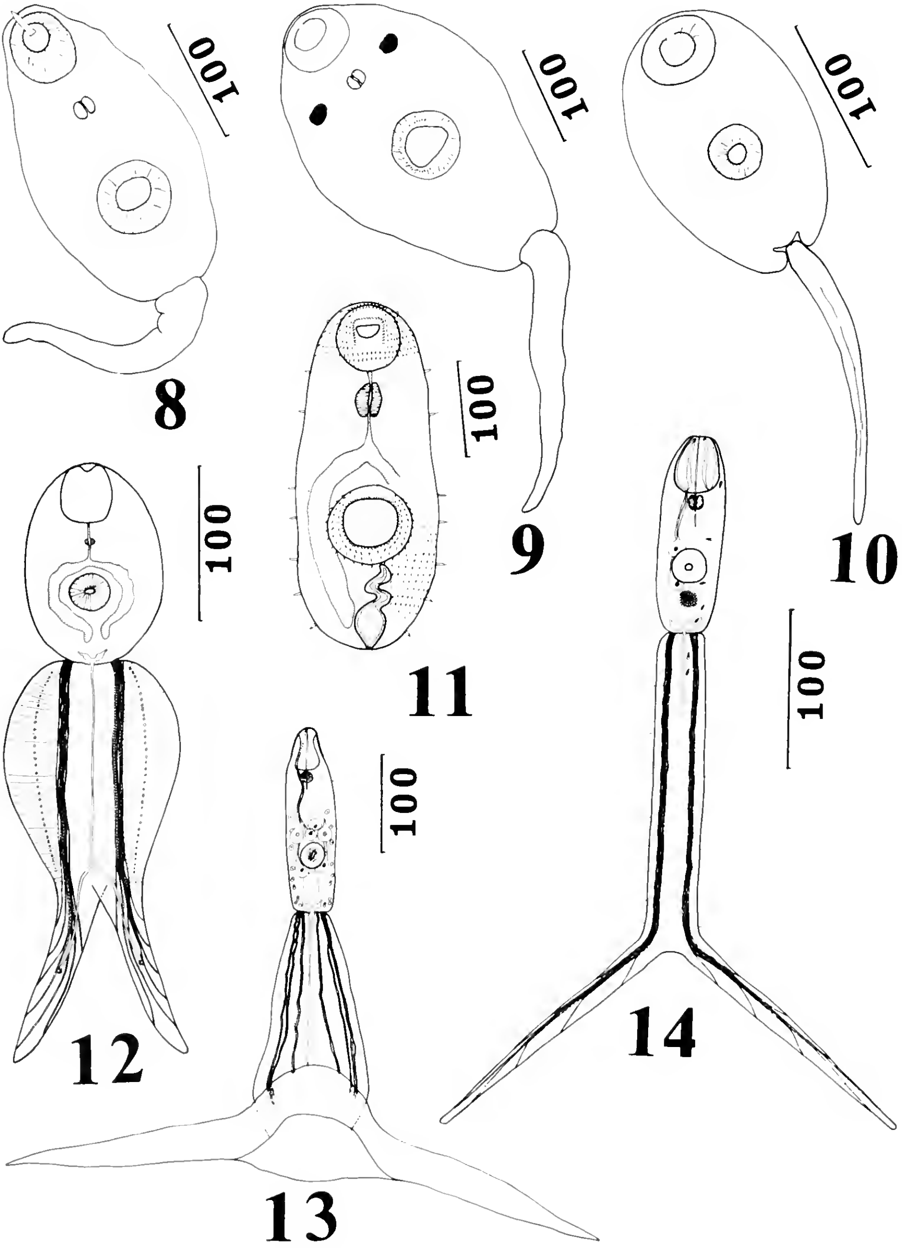
Description: Body 230-292(260) long by 102-144(123) wide. Tail 415-450(432) long by 35-46(40) wide. Oral sucker 118-

147(128) long. Acetabulum 40-77(57) long by 113-149(131) wide. Ceca thick walled, extend posteriorly to near level of excretory bladder. Paired excretory trunks containing many small concretions. Flame cell formula or number not determined.

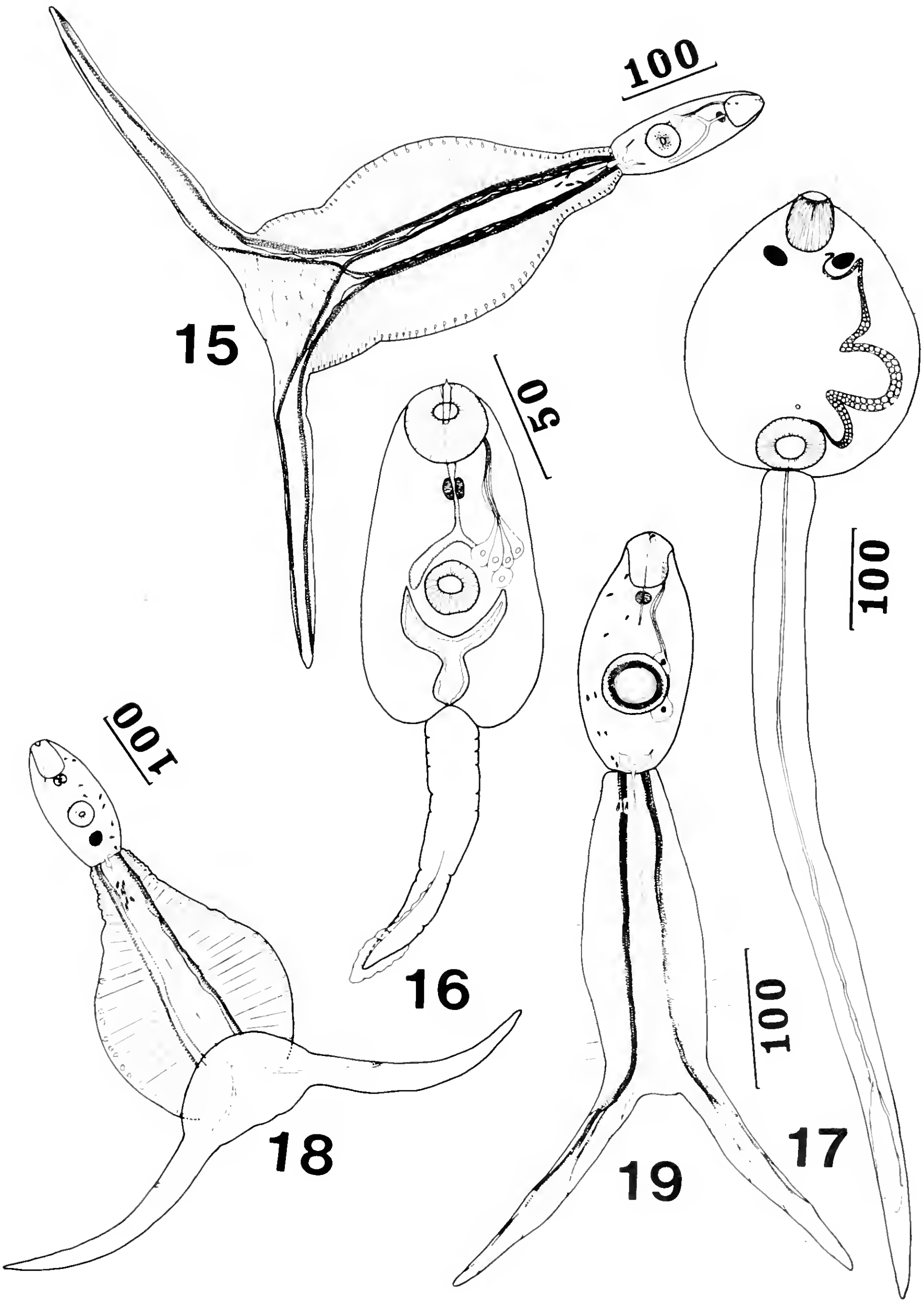


Figures 1-7. *Cercaria* types I-VII developing in southeastern Lousiana ancylid snails. Scale in microns.

Cercaria type II, although smaller, fits the description given by Krull and Price (1932) for the cercaria of *Megalodiscus temperatus*, and by Smith (1967) for larvae of that species developing in *Laevapex fuscus* and *Ferrissia fragilis* from Michigan. Smith reported an overall incidence of 14% for *F. fragilis*, whereas an inci-



Figures 8-14. *Cercaria* types VIII-XIV developing in southeastern Louisiana ancylids. Scale in microns.



Figures 15-19. *Cercaria* types XV-XIX developing in southeastern Louisiana ancylids. Scale in microns.

dence of only 1% was noted for infections in *L. fuscus*. Cercarial production in Michigan *F. fragilis* was in two distinct waves, one in spring and the other in autumn (Smith, 1967).

Like Smith, we noted a disparity in incidence of infection among the two limpet species. Of almost 5,000 *Laevapex fuscus* examined from SOR, only one harbored infection with *Megalodiscus temperatus*, while eight of 40 *Ferrissia fragilis* were infected. Two waves of cercarial production were observed. One began in late fall and continued until early spring, while the other began in early summer.

Cercaria Type III (Figures 3, 20, 22, 23, and 24)

Longifurcocercous, apharyngeate, monostome cercariae, with small eyespots, were found developing in all three limpet species and were collected at all localities except BPB.

Description: Body 179-207(194) long by 31-39(34) wide, with 12 annulations between oral sucker and acetabular anlagen. Two pairs of lateral setulae on posterior body near junction of tail stem. Tail stem 202-246(232) long by 26-37(31) wide, with five pairs of lateral setulae grouped near junction with body, and six or seven pairs grouped near bifurcation. Caudal bodies not observed in tail stem. Furcae 161-207(196) long by 16-23(17) wide, with delicate finfolds originating at level of excretory pores, which emptied on anterior surface of furcae. Oral sucker 37-55(46) long by 17-28(21) wide. Three pairs of penetration glands between eyespots and excretory bladder, with acetabular anlagen located immediately posterior to anterior pair. Genital primordium between posterior penetration glands and excretory bladder. Extent of ceca not determined. Eleven pairs of flame cells located in body and two pairs in tail.

Cercaria type III resembles the larva of *Posthodiplostomum minimum* (MacCallum, 1921), a parasite of the heron, *Nycticorax nycticorax* (Linnaeus, 1758). Two morphologically different cercariae have been described for *P. minimum*. Miller (1954) described *Cercaria minimum*, which bears similarity to *Cercaria* type III; however, Miller noted the presence of five pairs of caudal bodies in the tail stem, and 10 pairs of flame cells in the body and tail. *Cercaria minimum* Miller, 1954 developed in naturally infected *Physa heterostropha* Say, 1817 in Michigan. More recently, Bedinger and Meade (1967) reported on the life cycle of *Posthodiplostomum minimum*, the cercaria of which developed in naturally infected *Physa halei* Lea, 1864 in Texas. Those cercariae lack caudal bodies, have "flagellets" in two groups on the tail stem, and have 13 pairs of flame cells in the body and tail.

On morphological grounds *Cercaria* type III, although somewhat larger, more nearly resembles the cercaria described by Bedinger and Meade; however, in size, it resembles *Cercaria minimum*.

Cercaria Type IV (Figures 4, 20, 21, 22, 23, and 24)

Longifurcocercous, pharyngeate, distome cercariae were found developing in all three species of limpets and were collected at all five localities.

Description: Body 119-178(151) long by 41-62(51) wide, with anteriorly directed needle-like spines extending posteriorly to level of pharynx, and with three pairs of lateral papillate setulae. Tail stem 228-364(316) long by 72-98(77) wide, with four pairs of lateral setulae. Furcae 180-292 (239) long by 32-48(39) wide, with excretory pores opening at mid-length of posterior surface. Oral sucker 35-44 (39) long by 25-32(28) wide. Pharynx 9-12(10) long by 22-28(26) wide, with a single circle of inwardly directed, needle-like spines. Number and arrangement of penetration glands not determined. Ceca extended to postacetabular level. Six pairs of flame cells in body and two pairs in tail.

Cercaria Type V (Figures 5 and 20)

An echinostome cercaria, with spiny collar, was found developing only in *Hebetancylus excentricus* from BHF. Measurements of *Cercaria* type V used in the following description were taken from a single live specimen.

Description: Body 176 long by 148 wide, with an undetermined number of small collar spines. Tail without finfold, 392 long. Oral sucker 44 long by 44 wide. Acetabulum 50 long by 50 wide. Extent of ceca not determined. Many small concentrations restricted to middle and anterior portion of paired excretory trunks. Flame cell formula or number not determined.

Cercaria type V was collected only during June of the first summer and comprised 4.1% of the sampled *Hebetancylus excentricus* population (Figure 20).

Cercaria Type VI (Figures 6, 20, 21, 22, and 23)

Echinostome cercariae, without spiny collars, were found developing in all three limpet species at all localities except HIP.

Description: Body 168-196(184) long by 86-116(102) wide. Tail without finfold, 364-416(393) long by 43-53(46) wide, with pair of short flagellets near tip. Oral sucker 35-43(39) long by 38-43(40) wide. Acetabulum 37-50(43) long by 51-58(54) wide. Extent of ceca not determined. Paired excretory trunks each contain three or four large concentric concretions restricted to pre-acetabular region. Thirteen pairs of flame cells present in body.

Cercaria type VI may be a species of *Echinochasmus* Dietz, 1909, since cercariae of this genus often lack collar spines, have few and large excretory concentrations, and have short flagellets on the tail (Yamaguti, 1975).

Cercaria Type VII (Figures 7, 20, 21, and 22)

A brevifurcocercous, apharyngeate, distome cercaria of the turtle blood fluke family Spirorchiidae Stunkard, 1921 was found developing only in *Ferrissia fragilis* from BHF, BPB, and RAM.

Description: Body 192-256(219) long by 58-72(64) wide at acetabulum, with three pairs of lateral setulae. Anterior third of oral sucker covered with dense, fine spines. Spines around acetabulum large and numerous. Remainder of body covered with minute, sparse spines. Tail stem attached subterminally, 568-680(590) long by 52-67(60) wide. Short lateral setulae on tail stem arranged in two groups of nine pairs each. Anterior group all nonpapillate. Posterior group with last three pairs papillate. Furcae 200-268(227) long, with finfolds along margin. Oral sucker 44-69(60) long by 28-37(34) wide. Acetabulum protrusible, 24-30(28) long by 26-32(28) wide. Eyespots in second quarter of body. Five pairs of penetration glands from posterior margin of eyespots to fourth quarter of body. Sixth pair of fused glands in fourth quarter. Ceca extend to level of acetabulum. Five pairs of flame cells in body and one pair of large flame cells in tail. Under laboratory conditions cercariae emerged mostly at night. Life cycle studies (Turner and Corkum, 1977) indicated *Cercaria* type VII to be the larva of *Spirorchis scripta*.

Cercaria Type VIII (Figures 8 and 22)

A xiphidiocercaria of the *armatae* group parasitized only *Ferrissia fragilis* from RAM. Measurements from the following description were taken from a single living specimen.

Description: Body 252 long by 140 wide. Tail 203 long by 42 wide. Oral sucker 69 long by 64 wide. Stylet unshouldered, 25 long. Acetabulum 53 long by 64 wide. Extent of ceca not determined. Excretory bladder Y-shaped. Arrangement and number of flame cells or penetration glands not determined.

Cercaria Type IX (Figures 9 and 22)

An ophthalmoxiphidiocercaria of the family Allocreadiidae was found developing only in *Laevapex fuscus* collected at RAM. Measurements for the following description were taken from a single living specimen.

Description: Body 328 long by 228 wide at acetabulum. Tail 270 long by 43 wide. Oral sucker, with five rows of small, blunt spines forming a semicircle below mouth, 56 long by 69 wide. Acetabulum with two alternating circles of small, blunt spines, 64 in diameter. Stylet short and blunt. Eyespots in first quarter of body. Extent of ceca not determined. Number and arrangement of flame cells or penetration glands not determined.

According to Dr. Lewis E. Peters (1975, pers. comm.), *Cercaria* type IX appears "very similar to the cercaria that [he and Dr. J. Teague Self] studied in Oklahoma in the early 1960's." Peters also noted that he and Dr. Raymond Cable had confirmed identity of the cercaria, which also occurred in *Laevapex* from Indiana, to be that of *Allocreadium ictaluri*. Although Peters and Self (1963) reported *L. fuscus* as one of several second intermediate hosts, we were unable to find any harboring allocreadiid metacercariae among the 3,663 *L. fuscus* examined from RAM.

Cercaria Type X (Figures 10 and 23)

A small xiphidiocercaria of the *armatae* group, designated *Cercaria* type X, was found developing only in *Laevapex fuscus* at SOR.

Description: Body 152-182(169) long by 74-90(86) wide. Caudal pocket present. Tail 106-140(123) long by 30-37(35) wide. Acetabulum 24-28(26) long by 23-28(25) wide. Stylet slightly shouldered, 23-27(26) long. Extent of ceca not determined. Excretory bladder Y-shaped. Flame cell formula or number not determined. Penetration gland number and arrangement not determined. Pharynx, although present, was not observed.

Cercaria Type XI (Figures 11 and 22)

Tailless cercariae (cercariaea) of the family Lissorchiidae Poche, 1926 were found developing in *Laevapex fuscus* and *Ferrissia fragilis* at RAM.

Description: Body 324-392(358) long by 80-128(101) wide, with nine pairs of lateral papillate setulae. Pharynx 24-28(26) long by 26-31(29) wide. Oral sucker 50-64(54) long by 51-61(57) wide, with mouth surrounded on three sides by two alternating rows of small, inwardly directed spines. Acetabulum 58-69(63) long by 58-71(64) wide, with two alternating circles of small, inwardly directed spines surrounding inner rim, and a third row present on anterior quadrant of inner rim. Tegument with larger spines directed posteriorly; however, spines absent from area between oral sucker and acetabulum. Ceca extend to near base of excretory bladder. Excretory bladder cylindrical and thick walled. Flame cell and penetration gland number and arrangement not determined.

Cercaria type XI resembles *Cercariaeum* type I described by Duncan and DeGiusti (1976); however, it differs in host specificity (not restricted to *Laevapex fuscus*), in size (slightly larger than *Cercariaeum* type I), in arrangement of lateral papillate setulae, and in number and arrangement of small spines on the oral sucker and acetabulum.

Duncan and DeGiusti (1976) noted that papillae pattern and number were variable; however, tegumental spination pattern was fixed. Differences in size may be attributable to techniques used by these authors, since they first relaxed emergent cercariae in menthol solution prior to fixing in hot 10% formalin. They also measured cercariae in groups of twenty under a "floating" coverslip.

Cercaria Type XII (Figures 12 and 21)

A longifurcocercous, pharyngeate, distome cercaria was found developing only in *Hebetancylus excentricus* from BPB.

Description: Body 108-156(131) long by 62-99(83) wide. Tail stem 108-200(149) long by 83-150(108) wide. Furcae 104-163(124) long. Oral sucker 35-48(41) long by 29-39(34) wide. Acetabulum 23-29(25) long by 23-30(26) wide. Ceca surround acetabulum and extend to post-acetabular position. Tail, as seen in lateral view, appearing as a pair of empty, pressed trousers with excretory pores opening on inner surface of furcae. Number and arrangement of flame cells and penetration glands not determined.

Cercaria Type XIII (Figures 13, 20 and 24)

A longifurcocercous, pharyngeate, distome cercaria parasitized only *F. fragilis* from HIP and BHF.

Description: Body 164-220(193) long by 41-58(46) wide. Tail stem 288-316(297) long by 172-196(186) wide at bifurcation. Furcae 220-268(248) long by 40-60(48) wide. Oral sucker 44-58(51) long by 25-39(28) wide. Pharynx 12-14(13) long by 14-18(17) wide. Acetabulum with three circles of blunt, concentrically placed spines, 25-32(30) long by 30-35(32) wide. Three pairs of penetration glands, two pre- and one post-acetabular. Several smaller pairs of cells scattered throughout the body. Genital primordium between posterior penetration glands and excretory bladder. Extent of ceca not determined. Anterior body to level of pharynx covered with small, dense spines. Flame cell formula or number not determined. Tegument on tail stem at bifurcation formed into loose, bladder-like "skirt" continuous with furcae. "Skirt" most evident when cercariae were placed under coverslip pressure. Figure 13 was drawn without coverslip pressure and shows "skirt" in folded configuration.

Cercaria Type XIV (Figures 14 and 20)

A longifurcocercous, pharyngeate, distome cercaria was found developing only in *Ferrissia fragilis* from BHF.

Description: Body 112-153(127) long by 32-51(44) wide, with small dense spines to level of mid-oral sucker. Tail stem 187-220(207) long, with nine pairs of lateral setulae. Furcae 162-189(179) long by 14-18(16) wide. Oral sucker 32-41(37) long by 26-34(30) wide. Acetabulum 18-21(20) long by 19-25(23) wide, with two alternating circles of small, blunt spines. Two pairs of penetration glands, one pre-acetabular the other post-acetabular. Genital primordium between posterior pair and excretory bladder. Extent of ceca not determined. Five pairs of flame cells in body and two pairs in tail.

Cercaria Type XV (Figures 15 and 24)

A single *Ferrissia fragilis* collected at HIP was found to harbor infection with a longifurcocercous, pharyngeate, distome cercaria.

Description: Body 132-188(161) long by 34-52(41) wide, with small, dense spines to level of mid-oral sucker, less densely spined to level of gut bifurcation. Tail stem 280-336(305) long by 124-152(140) wide. Furcae 220-276(252) long by 28-46(35) wide. Oral sucker 35-52(45) long by 20-30(25) wide. Acetabulum 25-30(27) long by 28-32(30) wide, with three alternating circles of short, blunt spines. Ceca extend to mid-acetabulum. Two pairs of penetration glands, one pre- and the other post-acetabular. Muscle fibers from median portion of each fiber tract in tail stem contralateral in furca and form a chiasma anterior to bifurcation. Lateral fibers ipsilateral. Two pairs of flame cells in tail. Flame cell number or arrangement for body not determined.

Cercaria Type XVI (Figures 16 and 20)

A single *Ferrissia fragilis* collected at BHF was found to harbor infection with a small xiphidiocercaria of the *ornatae* group.

Description: Body 108-150(130) long by 58-72(64) wide. Tail with finfold, 90-122(108) long by 18-23(20) wide. Oral sucker 32-35(33) long by 30-35(32) wide. Acetabulum 18-23(21) long by 21-23(22) wide. Stylet shouldered 16-21(19) long. Five pairs of penetration glands and ceca extend to mid-acetabular level. Excretory bladder cellular and Y-shaped. Flame cell formula or number not determined.

Cercaria type XVI may be the larva of the frog lung fluke *Haemaetoloechus breviplexus*. In size of body and tail it appears intermediate between that noted by Schell (1965) for *H. breviplexus* larvae developing in experimentally infected *Gyraulus similaris* in Idaho, and that reported by Underwood and Dronen (1977) for those in an unknown species of experimentally infected *Ferrissia* from Texas. All other measurements, however, agree with those of Schell.

Cercaria Type XVII (Figures 17 and 21)

Heavily pigmented amphistome cercariae of the *pigmentata* group were found developing in *Ferrissia fragilis* from BPB, and *Laevapex fuscus* from RAM.

Description: Body 256-352(281) long by 160-273(233) wide, with 12 pairs of lateral setulae arranged along anterior half. Tail 506-800(702) long by 48-68(57) wide. Oral sucker 51-72(61) long by 48-69(54) wide. Acetabulum subterminal, 58-83(73) long by 62-101(85) wide. Eyespots large and oval, located in anterior quarter of body. Extent of ceca not determined. Paired excretory trunks filled with concretions and extending anteriorly with several coils until reaching level of oral sucker before turning posteriorly. Flame cell formula or number not determined. Cercariae maintained under laboratory conditions emerged only in morning, within five minutes after exposure to light, and quickly encysted on green vegetation.

Cercaria type XVII most nearly resembles the cercaria of *Stichorchis subtriquetrus* (Rudolphi, 1814), a cecal parasite of the beaver, *Castor canadensis* Kuhl, 1820. Bennett and Humes (1939) reported on the pre-cercarial development of this species in experimentally infected lymnaeid snails, *Lymnaea parva* Lea, 1841, in Louisiana. Bennett and Allison (1958) later obtained cercariae from experimentally infected *L. parva*; however, these authors suggested that this snail was not a satisfactory host because of high mortality among infected individuals.

Except for a slightly shorter tail, *Cercaria* type XVII fits the description for *S. subtriquetrus* given by Orloff (1941) for cercariae obtained from naturally infected *Planorbis vortex* (Linnaeus, 1758), *Lymnaea ovata* (Draparnaud, 1805), the operculate hydrobiid, *Bithynia tentaculata* (Linnaeus, 1758), and the terrestrial snail, *Succinea putris* (Linnaeus, 1758), in Russia.

Cercaria Type XVIII (Figures 18 and 24)

A single *Ferrissia fragilis* from HIP was found to harbor infection with a longifurcocercous, pharyngeate, distome cercaria.

Description: Body 150-184(166) long by 48-62(56) wide, with two pairs of lateral setulae, one pair near mouth and another papillate pair at level of excretory bladder. Anterior body to level of mid-oral sucker covered with small, dense spines. Tail stem 240-316(297) long by 128-172(160) wide, with two groups of lateral setulae, two pairs near junction with body and four pairs near bifurcation. Furcae 208-268(243) long, with excretory pores opening on anterior surface of mid-length. Oral sucker 40-44(42) long by 28-35(30) wide. Acetabulum 28-32(30) long by 30-35(33) wide, with several alternating circles of small, blunt concentrically placed spines. Extent of ceca not determined. Number and arrangement of penetration glands not determined; however, one pair pre-acetabular. Genital primordium between acetabulum and excretory bladder. Nine pairs of flame cells in body and three pairs in tail. Tegument on tail stem at bifurcation formed into loose, bladder-like "skirt" continuous with furcae.

Presence of three pairs of flame cells in the tail stem seems to be a deviation from a maximum of two pairs noted for other cercariae of this type (Yamaguti, 1975). Since only nine pairs were observed in the body, perhaps one pair in the tail may have originally been derived from the body complement.

Cercaria Type XIX (Figures 19 and 24)

A single *Ferrissia fragilis* from HIP was found to harbor infection with a longifurcocercous, pharyngeate, distome cercaria.

Description: Body 148-204(170) long by 56-96(76) wide. Tail stem 248-284(256) long by 80-101(90) wide, with 10 pairs of lateral setulae. Furcae 208-220(213) long by 22-32(27) wide, with excretory pores opening on posterior surface. Oral sucker

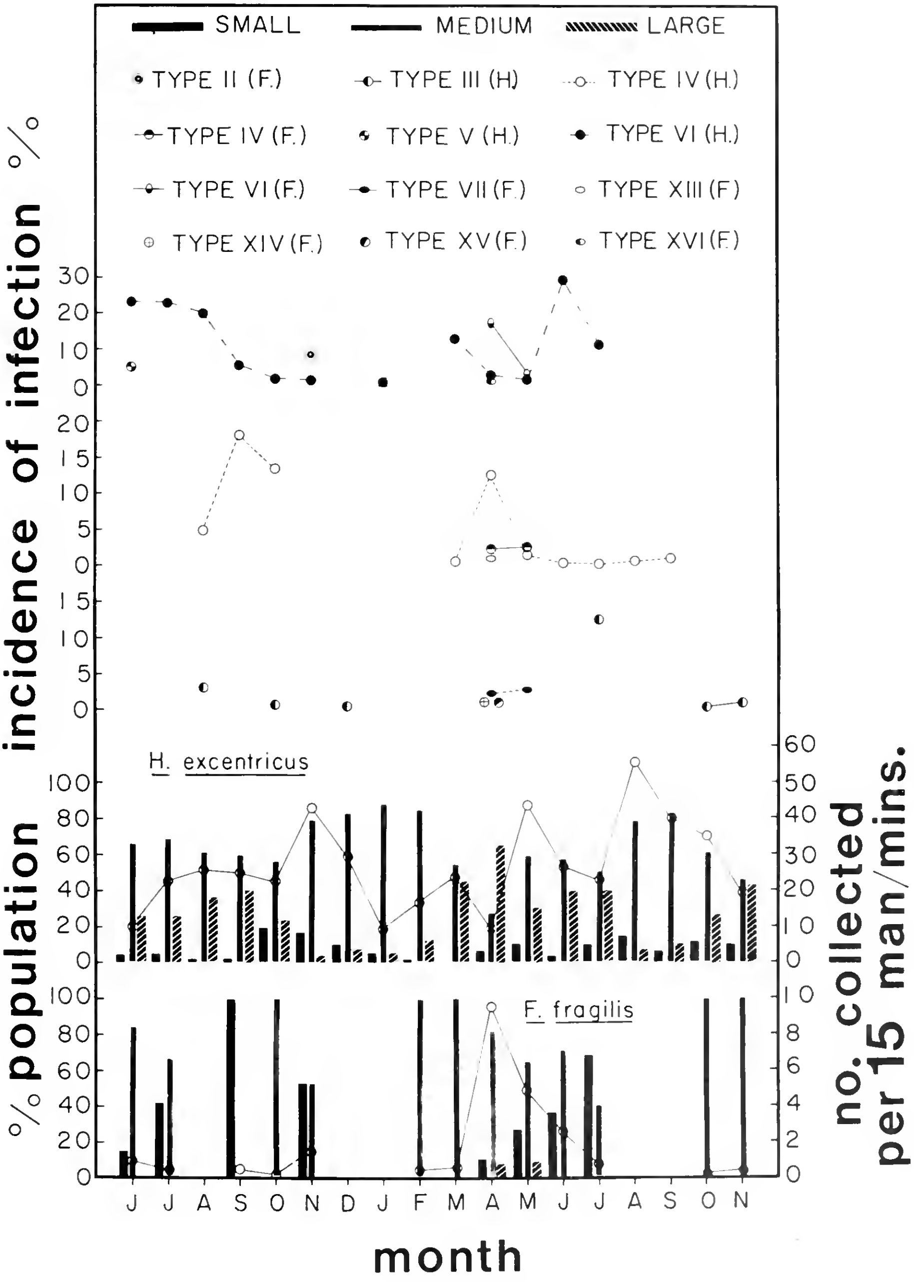


Figure 20. Monthly incidence of infection, population structure, and index of relative abundance for (H.) *Hebetancylus excentricus* and (F.) *Ferrissia fragilis* at Ben Hur Experimental Farm. Small, medium, and large refer to size classes of limpets. Cercarial type and limpet host combinations are indicated by various symbols. Relative abundance is indicated by circle with unbroken line.

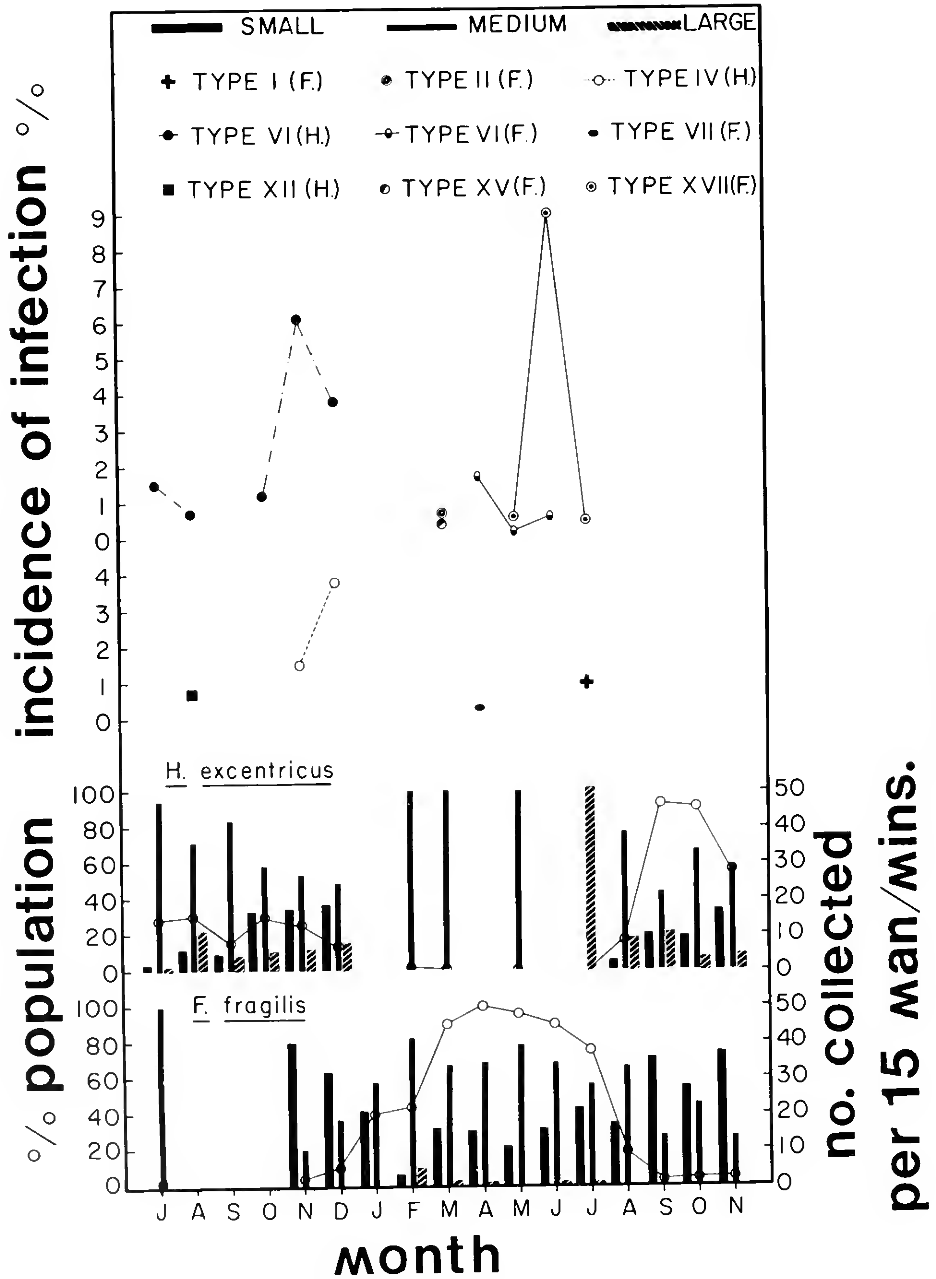


Figure 21. Monthly incidence of infection, population structure, and index of relative abundance for (H.) *Hebetancylus excentricus* and (F.) *Ferrissia fragilis* at Beaver Pond Branch.

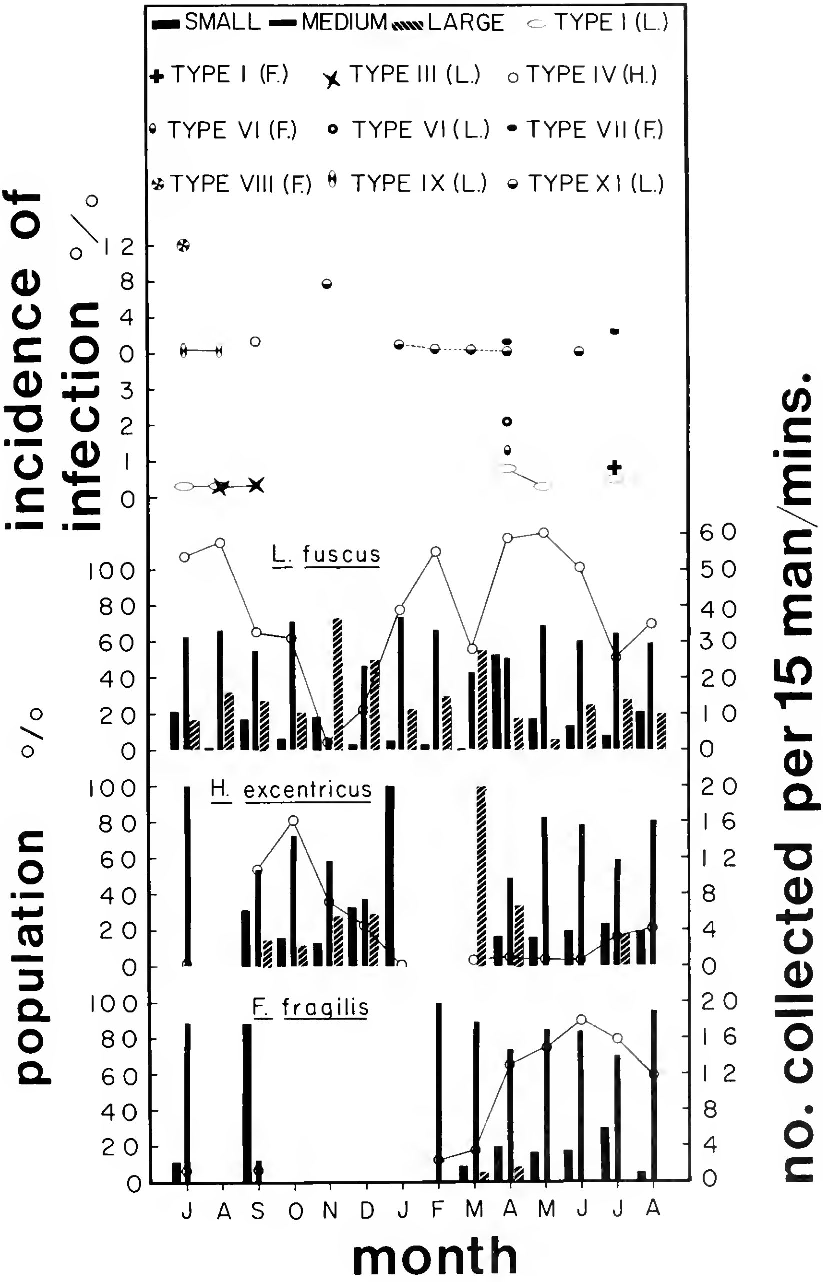


Figure 22. Monthly incidence of infection, population structure, and index of relative abundance for (L.) *Laevapex fuscus*, (H.) *Hebetancylus excentricus*, and (F.) *Ferrissia fragilis* at Ramah.

39-51(45) long by 30-39(35) wide. Pharynx 12-15(14) long by 14-17(16) wide. Acetabulum 48-57(52) long by 46-62(51) wide, with six circles of small, blunt spines around inner rim. Extent of ceca not determined. Two pairs of penetration glands, one pre- and the other post-acetabular. Ten pairs of flame cells in body and two pairs in tail.

DISCUSSION

Ecology of Southeastern Louisiana Ancylids

Although *Ferrissia fragilis* accounted for only 15% of the total ancylids collected and examined, it occurred at all sampled habitats. In contrast, *Laevapex fuscus*, which comprised 45% of the ancylids studied, was restricted to lentic habitats, and thus displayed greater ecological specialization. *Hebetancylus excentricus* was intermediate in ecological specificity because, although occurring at all habitats, it was not as successful, in terms of abundance, as *F. fragilis* at lotic BPB or *L. fuscus* at lentic SOR. McMahon (1976) stated this relationship when he noted, "representative species of these three limpet genera from the progressively less euryoecic series: *Ferrissia-Hebetancylus-Laevapex*."

Bivoltine and trivoltine reproductive patterns with overlapping generations, as exhibited by *Laevapex fuscus* and *Hebetancylus excentricus*, partially account for their predominance over *Ferrissia fragilis* at most habitats. Although McMahon (1976) noted a trivoltine pattern for a Texas *L. fuscus* population, we found no more than a bivoltine for southeastern Louisiana populations. Even at eutrophic SOR the reproduction-recruitment cycle occurred only twice during the 14-month survey.

Role of Southeastern Louisiana Ancylids in Trematode Ecology

Southeastern Louisiana ancylids play a major role in trematode life cycles because collectively they host at least 19 cercarial species, which in turn utilize five classes of vertebrates as definitive hosts.

Expectedly, the ecology of trematode intramolluscan stages was closely related to the ecology of the limpet hosts. Nowhere was this more evident than BHF (Figure 20), where the bivoltine reproduction of *Hebetancylus excentricus* was reflected in two cycles of cercarial production. The winter discontinuity in cercarial production reflected an interim between limpet cycles. Seasonality of those cercariae developing in *Ferrissia fragilis* did not demonstrate biannual patterns. Rather, individual trematode species were seasonal with discrete annual periods of cercarial production.

At BPB (Figure 21) the annual generation of each limpet species is reflected in an annual generation of cercaria production. *Cercaria* type XVII (probably *Stichorchis subtriquetrus*) from this locality demonstrated a pronounced seasonality, which must also relate to the life history of the beaver. Lowery (1974) noted that, although little is known about reproduction in Louisiana beaver, young are thought to be born in April or May. If true, June cercarial emergence and encystment on aquatic vegetation may be correlated with feeding habits of recently weaned beaver, and thereby insured infection of a presumably more susceptible individual.

A similar seasonal correlation between cercarial emergence and life history of definitive host may exist for *Cercaria* type VII (*Spirorchis scripta*) and the turtle, *Chrysemys scripta* (Schoepff, 1793). Cagle (1950) reported egg hatching in Louisiana *C. scripta* to occur from early July to early September. Peak cercarial emergence in July probably insures infection of young, susceptible individuals, not previously exposed or harboring a current infection with this blood fluke.

Differences in population biology of *Laevapex fuscus* at RAM and SOR were earlier attributed to putative differences in primary productivity between these habitats. As shown in Figures 22 and 23, these differences are in turn reflected in

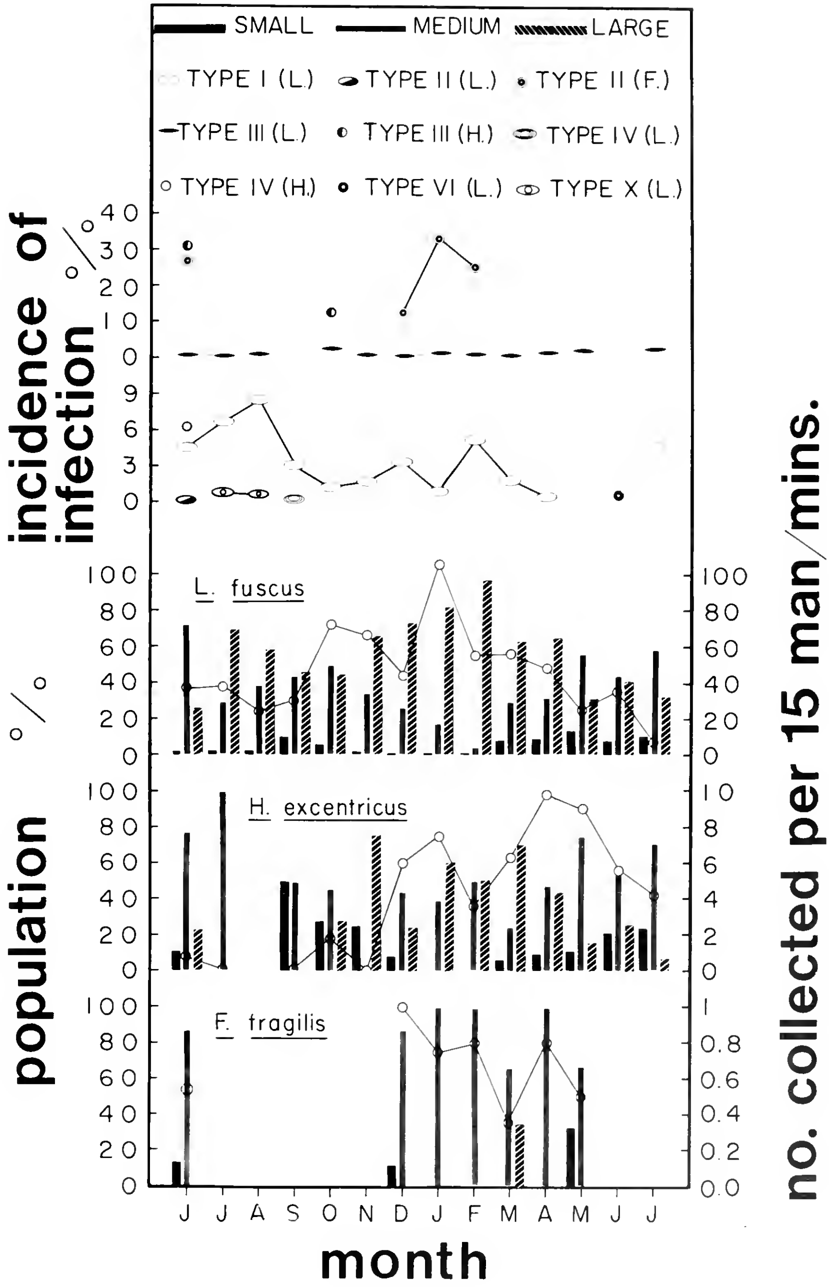


Figure 23. Monthly incidence of infection, population structure, and index of relative abundance for (L.) *Laevapex fuscus*, (H.) *Hebetancylus excentricus* and (F.) *Ferrissia fragilis* at Sorrento.

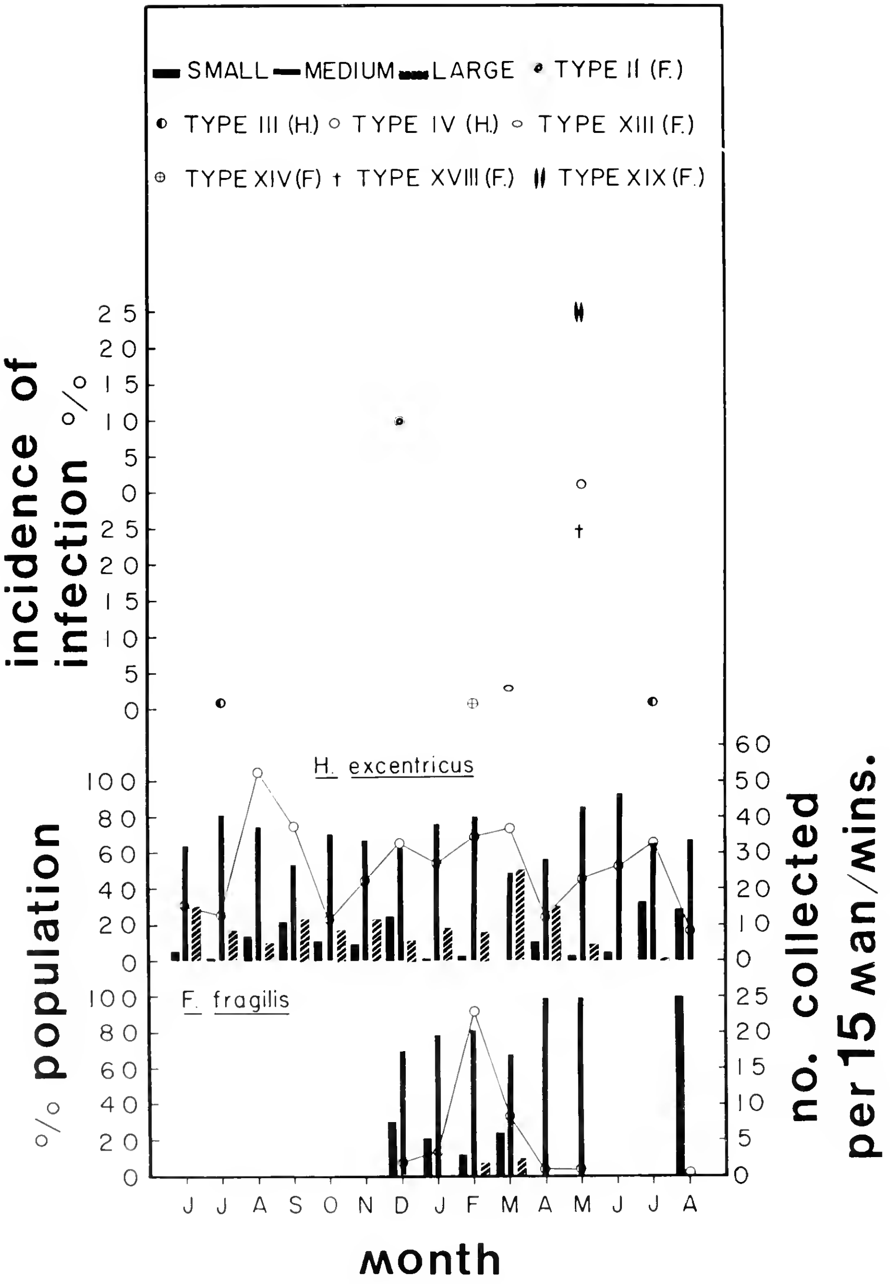


Figure 24. Monthly incidence of infection, population structure, and index of relative abundance for (H.) *Hebetancylus excentricus* and (F.) *Ferrissia fragilis* at Head of Island Pond.

the ecology of the respective trematode faunas. Seasonality of infection in *L. fuscus* at RAM was indicative of a single, annual host generation; however, two cercarial species were maintained essentially year round in SOR *L. fuscus*, and thus reflected relative stability in the *L. fuscus* population.

Head of Island Pond (Figure 24) was productive enough to permit a trivoltine pattern for *Hebetancylus excentricus*, but was faunistically poor in digenetic trematodes hosted by ancylids. Only seven host-parasite combinations were observed, as compared to 12 at BHF. Five of the seven involved the single generation of *Ferrissia fragilis*.

Differences in species composition of those trematode faunas hosted by ancylids can be explained on the basis of ecological differences in the habitats, i.e. absence or presence of suitable definitive or other hosts.

Phylogeny of Southeastern Louisiana Ancylids

Basch (1963) noted a general similarity in radular patterns among *Ferrissia, Laevapex,* and *Hebetancylus*. He also compared anatomy of certain "soft-parts" and noted a similar verge for *Hebetancylus* and *Ferrissia*; however, the *Hebetancylus* pseudobranch was bilobed like *Laevapex*. Basch thus proposed that *Hebetancylus* had greater affinity with *Laevapex*, which *he believed to be more advanced. Hebetancylus* and *Ferrissia* were suggested to have evolved independently from a common ancestor that was in turn derived from the family Planorbidae. However, Turner (1978) reported that *Hebetancylus*, like *Ferrissia*, formed a septum or horizontal calcareous shelf partially closing the shell aperture. This shell-like epiphragm, which was deposited by the posterior margin of the mantle, has not been reported for *Laevapex*. Because of this observation we believe that *Hebetancylus* and *Ferrissia* did not evolve independently and that *Hebetancylus* occupies an intermediate phylogenetic position between *Ferrissia* and *Laevapex*.

Digenetic trematodes generally exhibit greater host specificity for their molluscan first intermediate host than for subsequent hosts, perhaps because of a longer host-parasite evolutionary association (Pearson, 1972). In light of this generalization, we compared the trematode faunas hosted by each southeastern Louisiana ancylid species. Similarities and differences between respective faunas should reflect the emended phylogeny we have proposed.

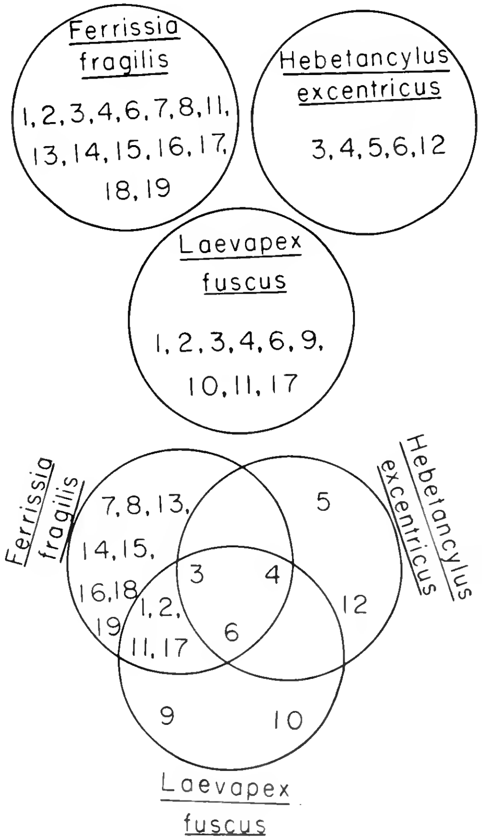


Figure 25. Southeastern Louisiana ancylid species as circles encompassing hosted cercariae and as overlapping circles encompassing "shared" and exclusively hosted cercariae.

Figure 25 depicts each of the three species as a circle encompassing hosted cercariae, which for convenience have been assigned arabic rather than conventional roman numeral designations. Figure 25 also demonstrates overlap or "sharing" of cercarial species.

Only an echinostome (type VI), a longifurcocercous distome (type IV), and *Cercaria* type III, tentatively identified as *Posthodiplostomum minimum*, were "shared" by all three limpet species. None were "shared" jointly by *Hebetancylus* and *Laevapex*, or by *Hebetancylus* and *Ferrissia*. *Ferrissia* and *Laevapex* jointly "shared" xiphidiocercaria (type I), *Megalodiscus temperatus* (type II), *Lissorchis* sp. (type XI), and *Stichorchis subtriquetrus* (type XVII).

Ferrissia seems to be the least specialized. Even though sympatric with the other genera, *Ferrissia* maintained the ability to host exclusively four times as many cercariae. This fact becomes more significant when noted that *F. fragilis* comprised only 15% of all limpets examined. Relative nearness of *Ferrissia* to the planorbid ancestral stock is suggested because at least five cercariae, hosted exclusively by *F. fragilis* or "shared" jointly with *Laevapex fuscus*, are also hosted by planorbids.

The relative positions of *Laevapex* and *Hebetancylus* are less clear. *Laevapex* and *Ferrissia* have more cercariae in common than *Hebetancylus* and *Ferrissia*; however, one cercaria (type XVII) is so broad in host specificity as to develop in prosobranch and both orders of pulmonate gastropods. Furthermore, on the basis of our study, and that of Smith (1967), *L. fuscus* does not appear to be as suitable host for *Megalodiscus temperatus* as does *F. fragilis*.

Laevapex fuscus and *Ferrissia fragilis* are widely distributed throughout the U.S. east of the Rocky Mountains (Basch, 1963; Clarke, 1973). Thus, the explanation for this "sharing" of cercariae by southeastern Louisiana *Laevapex* and *Ferrissia* may be found in the long sympatric association of these limpets in North America. Whereas, *Hebetancylus excentricus* is Caribbean in distribution with its historical, ecological associations in Central and South America, *H. excentricus* has been reported in North America from southern Florida, coastal Georgia (Basch, 1963), south central Texas (Pilsbry, 1889; Walker, 1903), north central Texas (McMahon and Aldridge, 1976), southern Oklahoma (McMahon, *et al.*, 1976), and southeastern Louisiana (Turner, 1978).

Finally, the fact that *Laevapex* hosts an allocreadiid (type IX), all others of which are hosted by sphaeriid clams, would tend to separate it from other ancylids and supports its placement in a highly derived phylogenetic position.

LITERATURE CITED

Basch, P.F. 1963. A review of the recent freshwater limpet snails of North America (Mollusca: Pulmonata). Bull. Mus. Comp. Zool., Harvard Univ. 129:339-461.

Bedinger, C.A., Jr. and T.G. Meade. 1967. Biology of a new cercaria for *Posthodiplostomum minimum* (Trematoda: Diplostomidae). J. Parasit. 53:985-988.

Bennett, H.J. and R. Allison. 1958. Observations on the life cycle of the trematode *Stichorchis subtriquetrus*. Proc. La. Acad. Sci. 20:10-13.

Bennett, H.J. and A.G. Humes. 1939. Studies on the precercarial development of *Stichorchis subtriquetrus* (Trematoda: Paramphistomidae). J. Parasit. 25:223-231.

Cagle, F.R. 1950. The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). Ecol. Monogr. 20:31-54.

Clarke, A.H. 1973. The freshwater molluscs of the Canadian Interior Basin. Malacologia. 13:1-509.

Cort, W.W. 1918. A new cercariaeum from North America. J. Parasit. 5:86-91.

Duncan, B.L. and D.L. DeGiusti. 1976. Three new lisorchiid cercariaea of the mutabile group from *Laevapex fuscus* (Adams, 1841) and *Ferrissia rivularis* (Say, 1917). Proc. Helminthol. Soc. Wash. 43:1-9.

Goodchild, C.G. and D.E. Kirk. 1960. The life history of *Spirorchis elegans* Stunkard, 1923 (Trematoda: Spirorchiidae) from the painted turtle. J. Parasit. 46:219-229.

Holliman, R.B. and J.E. Fisher. 1968. Life cycle and pathology of *Spirorchis scripta* Stunkard, 1923 (Digenea: Sprirorchiidae) in *Chrysemys picta picta*. J. Parasit. 54:310-318.

Krull, W.H. and H.F. Price. 1932. Studies on the life history of *Diplodiscus temperatus* Stafford, from the frog. Occ. Pap. Mus. Zool. Univ. Michigan 237:1-37.

Lowery, G.H., Jr. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State University Press, Baton Rouge. 565 p.

Malek, E.A. and T.C. Cheng. 1974. Medical and economic malacology. Academic Press, New York. 398 p.

McMahon, R.F. 1976. Growth, reproduction and life cycle in six Texan populations of two species of fresh-water limpets. Amer. Midl. Nat. 95:174-185.

________ and D.W. Aldridge. 1976. New distribution records for three species of freshwater limpet (Pulmonata: Ancylidae) from North Central Texas. Malac. Rev. 9:124-125.

________, ________, and G.L. King. 1976. New distribution records for two species of freshwater limpet (Pulmonata: Basommatophora) in southern Oklahoma. Southwestern Nat. 21:241-242.

Miller, J.H. 1954. Studies on the life history of *Posthodiplostomum minimum* (MacCallum, 1921). J. Parasit. 40:255-270.

Orloff, T.V. 1941. Investigation of the cycle of development of the trematode *Stichorchis subtriquetrus* Rud. parasitic in beavers. Comptes Rendus (Doklady) de l'Acad. des Sci. de l'U.R.S.S. 31:641-643.

Pearson, J.C. 1972. A phylogeny of life cycle patterns of the Digenea. pp. 153-189. *in*: Advances in parasitology. Vol. 10. Dawes, B. (Ed.) Academic Press, New York. 411 p.

Peters, L. and J.T. Self. 1963. An allocreadiid cercaria from limpets. (Abstr.) J. Parasit. 49 (Suppl.):41.

Pilsbry, H.A. 1889. Recent additions to the United States snail fauna. The Nautilus. 3:62-64.

Schell, S.C. 1965. The life history of *Haematoloechus breviplexus* Stafford, 1902 (Trematoda: Haplometridae McMullen, 1937), with emphasis on the development of the sporocysts. J. Parasit. 51:587-593.

Smith, R.J. 1959. Ancylid snails: first intermediate host to certain trematodes with notes on ancylids as a new host for *Megalodiscus* and *Haematoloechus*. Trans. Amer. Micro. Soc. 78:228-231.

________. 1967. Ancylid snails as intermediate hosts of *Megalodiscus temperatus* and other digenetic trematodes. J. Parasit. 53:287-291.

________. 1968. Ancylid snails as first intermediate hosts of *Lissorchis mutabile* comb. n. (Trematoda: Lissorchiidae). J. Parasit. 54:283-285.

Turner, H.M. 1978. *Hebetancylus excentricus* (Morelet) (Pulmonata: Ancylidae) in Louisiana and a report of septum formation. The Nautilus. 92:83-85.

________. and K.C. Corkum. 1977. New snail host for *Spirorchis scripta* Stunkard, 1923 (Digenea: Spirorchiidae) with a note on seasonal incidence. Proc. Helminthol. Soc. Wash. 44:225-226.

Underwood, H.T. and N.O. Dronen. 1977. The molluscan intermediate hosts for species of *Haematoloechus* Looss 1899 (Digenea: Plagiorchiidae) from raniid frogs of Texas. J. Parasit. 63:112.

Walker, B. 1903. Notes on eastern American ancyli. The Nautilus. 17:13-19, 25-30.

Wallace, H.E. 1941. Life history and embryology of *Triganodistomum mutabile* (Cort) (Lissorchiidae: Trematoda). Trans. Amer. Micro. Soc. 60:309-326.

Yamaguti, S. 1975. A synoptical review of life histories of digenetic trematodes of vertebrates. Keigaku Publ. Co., Ltd., Tokyo. 1100 p.

ECOLOGICAL MORPHOLOGY OF FRESHWATER STREAM FISHES

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ABSTRACT

Variation and interrelations of 56 morphological features were studied in 44 species of stream-living fishes. The morphological characters are interpreted ecologically based on information in the literature, character correlations, factor analysis, gut content analyses, and field observations.

The results show extensive significant linear correlations among many of the characters. A number of multiple associations were identified and ranked in the factor analysis. The ecological meanings of these latter results are that the major morphological trends in these fishes are: (1) differentiation in feeding strategy between "lie-in-wait" biting predators and cruising suction feeders; (2) habitat separation according to water velocity; (3) vertical habitat separation; and (4) feeding differentiation between small insectivores and large omnivores.

Gut content data were also examined by factor analysis. The results showed that for these freshwater stream fishes, size of prey is the most important component in separating the diets of different species and vertical position of the prey is the second most important component. Various correlations between the size and location of the prey and several morphological characteristics are also discussed.

How much about the biological roles of a species is determinable from its anatomical features and what particular functions are regularly associated with which features? These twin questions are at the heart of much current work in the areas of functional and ecological morphology (Bock and von Wahlert, 1965; Hespenheide, 1973). The purpose of the research presented here is to provide some answers to these questions for certain North Carolina freshwater stream fishes.

The relationship between the form of fishes and their life habits has been the subject of casual writings from at least the time of the ancient Hindus (Hora, 1935). More recently, Hubbs (1941) provided a good generalized background on this topic, and subsequent works by Alexander (1967), Aleev (1969), and Gosline (1971) provide modern and comprehensive summaries of various aspects.

In this paper I (1) summarize earlier theoretical and experimental studies in the literature relevant to probable functional interpretation of various morphological features of fishes and (2) present the results of my own research using correlation analysis, factor analysis, and gut content analysis on these same morphological features. Additional discussion of the structure of stream fish communities based on this morphological assessment of ecological roles is presented elsewhere (Gatz, 1979).

MATERIALS AND METHODS

Fishes and Streams.—Seines of various lengths were used to collect fishes at six stations in each of three streams in the Piedmont of North Carolina. The streams sampled were East Prong Little Yadkin (Stokes County, Pee Dee drainage), Mud Creek (Durham County, Cape Fear drainage), and Maho Creek (Person County, Roanoke drainage). Collections were made at all seasons over a two year

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period (August, 1972, through August, 1974). All species thus collected were included in the analysis of morphology.

Samples of ten adult individuals were measured for each of the 33 species for which I had collected sufficient material. These species were *Esox americanus*, the redfin pickerel, *Esox niger*, the chain pickerel, *Clinostomus funduloides*, the rosyside dace, *Hybopsis hypsinotus*, the highback chub, *Nocomis leptocephalus*, the bluehead chub, *Notemigonus crysoleucas*, the golden shiner, *Notropis alborus*, the whitemouth shiner, *Notropis altipinnis*, the highfin shiner, *Notropis analostanus*, the satinfin shiner, *Notropis ardens*, the rosefin shiner, *Notropis cerasinus*, the crescent shiner, *Notropis chiliticus*, the redlip shiner, *Notropis procne*, the swallowtail shiner, *Phoxinus oreas*, the mountain redbelly dace, *Semotilus atromaculatus*, the creek chub, *Castostomus commersoni*, the white sucker, *Erimyzon oblongus*, the creek chubsucker, *Ictalurus nebulosus*, the brown bullhead, *Noturus insignis*, the margined madtom, *Aphredoderus sayanus*, the pirate perch, *Gambusia affinis*, the mosquitofish, *Centrarchus macropterus*, the flier, *Lepomis auritus*, the redbreast sunfish, *Lepomis cyanellus*, the green sunfish, *Lepomis gibbosus*, the pumpkinseed, *Lepomis gulosus*, the warmouth, *Lepomis macrochirus*, the bluegill, *Micropterus salmoides*, the largemouth bass, *Pomoxis nigromaculatus*, the black crappie, *Etheostoma flabellare*, the fantail darter, *Etheostoma fusiforme*, the swamp darter, *Etheostoma olmstedi*, the tessellated darter, and *Perca flavescens*, the yellow perch. For the 11 rarer species, all individuals collected were used. These 11 species were *Anguilla rostrata*, the American eel, *Umbra pygmaea*, the eastern mudminnow, *Notropis hudsonius*, the spottail shiner, *Moxostoma anisurum*, the silver redhorse, *Moxostoma erythrurum*, the golden redhorse, *Moxostoma pappillosum*, the suckermouth redhorse, *Moxostoma robustum*, the smallfin redhorse, *Ictalurus catus*, the white catfish, *Ictalurus punctatus*, the channel catfish, *Enneacanthus gloriosus*, the bluespotted sunfish, and *Percina crassa*, the Piedmont darter. The conclusions drawn concerning the interpretation of the morphological features should not, however, be generalized to groups of fishes with grossly different structure or habitats.

Morphological Characteristics. – Fifty-six morphological characteristics were chosen for study. Determinations of 50 of these characters were made on each individual fish. In addition, six characters related to superficial brain morphology were measured on a single individual of each species. A preliminary study of the brains of several individuals of a single species (*Notropis altipinnis*) had indicated very low variance in these characters.

Each of the 56 characters is listed below along with the method of determination. All length measurements less than 120 mm were made with vernier calipers to the nearest 0.1 mm and length measurements longer than this were made with a millimeter rule. All area measurements were made from outline drawings using a planimeter. For all qualitative characters, the various manifestations or states of the characteristic were coded numerically using integers. These character state codes for qualitative characters are indicated in parentheses below where relevant.

Superficial body and body shape characters

1. Standard length in this study is the straight line distance from the most anterior part of the head to the terminus of the vertebral column.

2. Pigmentation pattern was visually classified into one of four qualitative categories: (1) silvery or reflective sides; (2) countershading with a dark lateral band; (3) mottled pattern or vertical bars; and (4) countershading without either silveriness or a lateral band.

3. Completeness of the lateral line canal was recorded as being complete (2), incomplete (1), or lacking (0).

4. Position of the lateral line canal was recorded as lacking (0), curving dorsally (1), horizontal (2), or curving ventrally (3).

5. Relative head length was measured as the straight line distance from the most anterior point on the upper lip to the posterior margin of the opercular membrane divided by the standard length. In large adult *Lepomis auritus*, the redbreast sunfish, excessive hypertrophy of the opercular membrane occurs. For this species the posterior limit for the head length measurement was taken at a point where a subjectively "reasonable" opercular membrane might end.

6. Flatness index is the maximum body depth divided by the maximum body width.

7. Relative body depth is the maximum body depth divided by the standard length.

8. Index of trunk shape is the perpendicular distance from the anterior tip of the head to an imaginary vertical line at the point of maximum body depth divided by the standard length.

9. Relative peduncle length is the horizontal distance from a vertical line at the level of the posterior margin of the base of the most posterior median fin to the terminus of the vertebral column divided by the standard length.

10. Caudal peduncle flatness index is the depth of the peduncle at its midpoint divided by the width at the same point.

Caudal fin characters

11. Aspect ratio of the caudal fin may be calculated as span squared divided by area (Nursall, 1958; Ovchinnikov, 1971). Span or maximum vertical distance and area were measured from an outline drawing of a maximally extended caudal fin.

12. Caudal span / body depth ratio is the span of the caudal fin divided by the maximum body depth.

13. Number of caudal fin rays is the total count of all rays reaching further than one half the distance from the base of the caudal fin to its distal edge. For fishes in the families Cyprinidae, Catostomidae and Centrarchidae, this count is the same as the count for caudal rays given by Hubbs and Lagler (1958), i.e., this count is the number of branched rays plus two (principal ray count). For fishes in other families such as Esocidae and Ictaluridae, some "rudimentary rays" (Hubbs and Lagler, 1958) were also counted. The number of "rudimentary rays" counted was determined by the length criterion set in this study. In the case of *Anguilla*, in which the rays of the dorsal, anal and caudal fins all form a continuous series, this character was not used.

Paired fin characters

14. Pectoral fin length is the distance from the base of the pectoral fin to the extreme tip of the fin at its longest point divided by the standard length of the fish.

15. Aspect ratio of the pectoral fin is estimated as a length to width ratio.

16. Relative pectoral fin area is the surface area of the pectoral fin divided by the surface area of the fish. Outline drawings of one pectoral fin and of the entire fish in lateral view were made by tracing around the objects. Relative pectoral fin area was taken to be the ratio of the areas of these two drawings.

17. Relative distance of the pectoral fin from the center of gravity of the fish was measured from the medial base of the pectoral fin to the point of center of gravity (CG) on the lateral surface of the fish and divided by standard length. This point CG was determined by balancing the fish on the tip of a dissecting needle. Notice that this distance can be small both when the fin is slightly anterior to the CG or posterior to the CG and thus is a different character than #19 below.

18. Pectoral fin shape was coded based on a subjective evaluation of whether the fins were (1) rounded, (2) intermediate, or (3) pointed.

19. Position of the pectoral fin relative to the center of gravity is an assignment of how the pectoral fin when adpressed against the lateral surface of the body relates to a transverse plane through the

point CG as defined above. Four possible relationships were recognized: (1) fin wholly anterior to the plane; (2) fin originating anterior to CG and extending posterior to the plane; (3) fin originating at the level of the CG plane; and (4) fin originating posterior to the CG.

20. Number of pectoral fin rays were counted on alizarin stained fins. All rays (including spines), no matter what length, were counted.

21. Pelvic fin length was measured in a manner strictly analogous to pectoral fin length (#14, above).

22. Aspect ratio of the pelvic fin was estimated as a length to width ratio.

23. Relative pelvic fin area was measured analogously to relative pectoral fin area (#16, above).

24. Relative distance of the pelvic fin from the center of gravity of the fish was measured analogously to the similar character, number 17, for the pectoral fin.

25. Pelvic fin shape was categorized similarly to pectoral fin shape.

26. Position of the pelvic fin relative to the center of gravity was an assignment using the same four character states as were used in the analogous character for the pectoral fin (#19, above).

27. Number of pelvic fin rays was counted like the number of pectoral fin rays.

28. Position of the dorsal fin relative to the center of gravity was an assignment using the same four character states as were used in the analogous character for the pectoral fin (#19, above). Assignment was made according to the position of the entire dorsal fin base relative to the CG plane.

Head characters

29. Relative eye size was the diameter of the eye between fleshy orbits along an anterior-posterior axis divided by the standard length.

30. Position of the eyes involved assigning character states depending upon whether the eyes were placed laterally on the head (1), or were oriented dorsolaterally either slightly (2) or greatly (3).

31. Eye pigmentation was a categorization according to the presence or absence and orientation of any dark bands of pigmentation running across the cheek and through the eye. Possible categories and their character state codes were: (0) no such pigment; (1) horizontal line through the eye; (2) vertical line through the eye; and (3) both horizontal and vertical lines through the eye.

32. Position of the mouth was coded according to the position of the opening of the mouth when closed. Character states were (1) supraterminal if the lower jaw extended anterior to the upper, (2) terminal if the jaws were subequal, (3) subterminal if the lower jaw ended slightly posterior to the upper, (4) inferior if the opening was clearly recessed from the anterior edge of the head, and (5) ventral if the mouth was positioned along the ventral surface of the body.

33. Orientation of the mouth was coded according to the orientation of an imaginary plane perpendicular to the longitudinal axis of the body and tangential to both lips of the open mouth. Character states were: (1) dorsal if the plane faced above the vertical, (2) anterior if the plane was vertical, (3) oblique if the plane faced obliquely downward, and (4) ventral if the plane was horizontal.

34. Relative width of the mouth was the interior lateral dimension of the opening when the mouth was fully opened, divided by the standard length of the fish.

35. Relative height of the mouth was the interior dorso-ventral dimension of the opening when the mouth was fully opened, divided by the standard length of the fish.

36. Index of protrusion was measured as the ratio of snout length with the mouth open to snout length with the mouth closed where snout length is the distance from the interior surface of the anterior edge of the bony orbit of the eye to the anterior margin of the upper jaw at its midpoint.

37. Number of barbels was the count of these sensory structures about the mouth.

38. Number of branchiostegal rays was a count of these structures which support the gill coverings. Alizarin staining was used to facilitate counting.

39. Presence of jaw teeth was coded (0) if none were present, (1) if teeth were on the mandible and premaxillary and/or maxillary only, and (2) if teeth were on both jaws and additional bones of the roof of the mouth such as the palatine or vomer.

40. Shape of jaw teeth was coded (0) if such teeth were absent, (1) if all teeth were small sharp points, and (2) if both small pointed and larger canine teeth were present.

41. Hypertrophy of teeth on the pharyngeal arches was coded (0) if all teeth on the fifth pharyngeal arch were small, and (1) if the teeth were hypertrophied.

42. Shape of the pharyngeal teeth was coded (1) if all teeth were short pointed structures, (2) if the teeth were hooked, (3) if the teeth had cutting edges, and (4) if the teeth had flattened grinding surfaces.

43. Number of gill rakers was a count of the total number of rakers which were visible after staining with alizarin on both ascending and descending limbs of the lateral surface of the first arch.

44. Shape of the middle gill raker was measured as the length divided by the width of that raker. In the case of pickerels, genus *Esox*, in which the gill rakers are represented by flat plates only, the length was taken to be zero and hence the value for this character was also zero.

45. Finer structure of the gill rakers was coded (0) if each raker was smooth, (1) if each raker had a ridged surface, (2) if each raker had fewer than 50 fine sharp teeth on it, and (3) if each raker had more than 50 fine teeth on it.

Internal body characters

46. Relative volume of the swim bladder was estimated by dividing the volume of the swim bladder by the volume of the fish. The latter volume was determined by measuring displacement volume. Swim bladder volume was measured in different ways in different families of fishes. In fishes such as cyprinids and catostomids in which the swim bladder could be removed intact, it was and then filled with water using a syringe and its displacement volume determined. In fishes which have swim bladders with rather rigid walls and definite median partitions such as centrarchids and ictalurids, the lateral portion of the left side of the bladder was removed and the volume of water required to fill the right half determined. Swim bladder volume was estimated to be twice this volume. For fishes like esocids which have thin walled, non-removeable swim bladders, the volume was estimated mathematically using the formula for the volume of a cylinder. The estimate of radius used was obtained from measurements of both lateral and dorso-ventral diameters of the swim bladder in a series of transverse sections of the entire fish.

47. Relative length of the swim bladder was the ratio of the length of the swim bladder to the standard length of the fish.

48. Relative gut length was measured as the length of the entire alimentary canal posterior to the pharynx divided by the standard length. The digestive tract was dissected from the fish and mesenteries and was then stretched slightly to straighten bends when the measurement was taken.

49. Number of pyloric caeca was a count of the caeca at the junction of the stomach and the intestine.

50. Percentage of red muscle in the caudal peduncle was estimated as a percentage of total muscle in transverse sections made near the middle of the peduncle. Sections were made using a freezing microtome, stained for fats (which are higher in concentration in red muscle than in white), and mounted on slides. Planimeter estimates of the areas of the red and white muscle were made on drawings of the slides traced from the image projected by a microprojector.

Brain characters

51. Relative size of the forebrain was determined by measurement of the length and the width of both forebrain lobes and

expressing the average of these two dimensions as a proportion of the same two measurements of the optic lobes. Brains were exposed dorsally, and thus this character was an estimate of the amount of the dorsal surface of the brain which was occupied by the forebrain relative to the amount occupied by the optic lobes.

52. Relative size of the optic lobes was determined by expressing the average of the length and width of these lobes as a proportion of the total length of the brain from the anterior end of the forebrain to the posterior end of the vagal lobes.

53. Relative size of the cerebellum is, as are all further brain characters, analogous to the character on the forebrain (#51, above) in that the average of the length and width of the lobe(s) under consideration is expressed in relation to the average of the length and width of the optic lobes.

54. Relative size of the vagal lobes, as indicated above, compares the dimensions of the vagal and optic lobes.

55. Relative size of the facial lobes compares the size of these lobes to the optic lobes.

56. Relative size of the acoustic tubercles compares the size of these lobes to the optic lobes.

Gut Content Analysis.—As an aid to the interpretation of the morphological characteristics, gut contents were examined throughout the entire length of the digestive tract of all individuals that were studied morphologically. Replacements were substituted for all fishes which had either completely empty tracts or tracts with wholly digested material. Each replacement was selected to be of as nearly as possible the same size and the same date of collection as the original fish.

Items found in the gut were identified as completely as possible. Grouped categories of food items were used in the final analysis of foods taken. These categories were: (1) fishes, (2) copepods, (3) ostracods, (4) aquatic insects, (5) terrestrial insects, (6) crayfishes, (7) isopods and amphipods, (8) diatoms, (9) filamentous algae, (10) molluscs, (11) non-insect terrestrial invertebrates, and (12) vascular plants. Size of food items (greatest linear dimension) was measured directly from intact items and was estimated from the dimensions of an identified part in the case of broken or digested organisms. The presence of sand and silt in the gut was recorded also.

Gut content data were coded to facilitate numerical treatment. Following in the tradition of fishery biology (Lagler, 1956), two ways of considering prey were recognized: number of items of a given category, and percentage volume of all food belonging to a given category. These two types of information were incorporated into the gut content characters by forming two characters for each of the 12 previously listed categories of food items. Frequency characters were given character state codes according to the scheme: (1) never taken, (2) present in up to 20% of tracts , (3) 21-40%, (4) 41-60%, (5) 61-80%, and (6) 81-100%. Percentage volumetric importance character state values were based on the percentage of digestive tracts examined in which item(s) of the given category formed a subjectively determined largest percentage volume of food of a single type, i.e., primary food. Character state values for these characters were: (1) not taken at all, (2) taken, but never the primary food category, (3) sometimes the primary food category, (4) taken more often as the primary food than items in any other category, but still not in the majority of individuals of the species, (5) primary food category in the majority of individuals, and (6) the only food utilized. The importance character and frequency character can be identical for any given category. This was the case for categories 7, 10, and 12 above, and in these cases I used only a single character representing both frequency and importance in subsequent analyses.

The prey size data were coded as two characters: absolute prey size and relative prey size. For both, the coded value for each species was derived from an estimated overall mean size of an item of prey. Character states for the absolute prey size character were: (1) $\leq$ 2 mm, (2) 5 mm, (3) 10 mm, (4) 20 mm, (5) 40 mm, and (6) $\geq$60 mm. For the relative prey size character, the estimated average absolute prey size was divided by the average standard length for the species sample to give a proportion. This was coded according to the scheme: (1) $\leq$ 0.05, (2) 0.10, (3) 0.15, (4) 0.20, (5) 0.25, and (6) $\geq$0.30.

Mathematical Methods

Simple linear correlations.—Two types of correlation coefficient were determined between the species means of all characters for all 33 common species. Pearson product-moment correlation coefficients were calculated using the Biomedical Computer Program BMD P1M. Spearman rank-order correlation coefficients were calculated with procedure Spearman of the Statistical Analysis System, North Carolina State University. The model underlying the former type requires that the two variables being correlated each exhibit a normal distribution. This was not the case for a number of the characters in this study; therefore, the latter type coefficient was also calculated because the model for it does not require that the variables fit any particular distribution.

The Bonferonni technique was used in assigning significance to the correlation coefficients. This is a very conservative procedure which allows one to know the probability of making a family Type I error. A Type I error is made if a hypothesis is rejected when it is true (in this case, the recognition of correlations as significant which are not). All statistical tests which employ the same set of observations belong to the same family. Thus, in the correlation analysis described here, the 55 correlations of each morphological character with every other character is a family of tests because the same set of observations is used 55 times. In order for the probability of making a Type I error to equal $P < 0.05$ in an entire family of tests, the Bonferonni technique requires that each individual test be conducted at a probability of $0.05 / n$ where n is the number of tests in the family. For the present study, $0.05 / 55$ is approximately equal to 0.001. Therefore, Pearson correlation coefficients were considered to be significant if they were greater than or equal to 0.546 ($df = 31$, $P < 0.001$) and Spearman correlation coefficients, if they were greater than or equal to 0.571 ($df = 31$, $P < 0.001$). This technique controls Type I errors because hypotheses of no relationship between two variables are rejected only at a very small value of P, i.e., when correlations are quite likely significant. Of course, the probability of making a Type II error (failure to reject a hypothesis when it is false, i.e., in this case, failure to recognize a significant correlation) is, as always, inversely related to the probability of making a Type I error.

Factor Analysis.—Factor analysis is a multivariate statistical technique that generates a small number of hypothetical factors which reproduce the linear correlations between variables in the original data set. Each factor so generated is a linear combination of covarying portions of the original variables. Interpretation of the hypothetical factors is facilitated by orthogonal rotation using the varimax criterion. Orthogonal rotation of the factors makes each factor statistically independent; i.e., the factors are not correlated. The varimax criterion maximizes the variance of each factor by causing as many factor loadings (i.e., coefficients relating the original variables to factors) as possible to tend toward zero or one. Thus each of the originally measured variables tends to make either a large or a negligible contribution to each of the hypothetical factors. The chief value of factor analysis is as an aid in the recognition of overall trends in the variation and covariation of a large number of variables. Additionally, because factor analysis also indicates the proportion of the total pattern of variation accounted for by each factor, it is of value in understanding the relative strength of trends in variation.

Factor analysis was performed in this study using Biomedical Computer Program BMD O8M. Orthogonal rotation using the varimax criterion was used. In accordance with the suggestion of Harman (1967), only factors with eigenvalues greater than one were considered. This prevents "overfactorization," i.e., the generation of hypothetical constructs that are explaining trends in error variances rather than in the pattern of variation in the original variables.

RESULTS AND DISCUSSION

In the first three sections below the results of the three major types of analyses are presented individually. Each analysis by itself provides some useful information in the understanding of fish morphology. In a fourth section, then, all these results are integrated with information from the literature in order to provide a functional, ecological interpretation of each of the morphological features studied.

Simple Linear Correlations.—Extensive correlations between characters were determined. Using the previously defined criterion for significance, 500 of the 3080 Pearson product-moment coefficients were significant as were 494 of the Spearman rank-order coefficients. However, 200 of these differed between types of coefficient. I tested whether part of the difference in result might have been due to differences in character distributions. The total set of characters was divided into two groups: those in which the values showed continuous variation (e.g., proportional measurements) and those in which the values were discrete (e.g., fin ray counts and qualitative characters with integer character state codes). Chi-square analysis was then used to test the null hypothesis that the two types of correlation coefficient acted at random with regard to these different types of characters. In both cases the hypothesis of randomness was rejected. Of correlations unique to the Spearman rank-order correlation coefficient, significantly more ($P < 0.005$) involved characters with discrete character state distributions than one should expect at random. Of correlations unique to the Pearson product-moment correlation coefficient, significantly more ($P < 0.05$) involved characters with continuous variation. However, visual examination of frequency plots of character state values indicated that characters with discrete character state distributions did not as a class necessarily show the greatest deviation from normal distributions. As a consequence of all this, I have somewhat arbitrarily listed below only the approximately 400 correlations determined to be significant by both types of coefficient. If the r in both cases was greater than 0.717 so that the coefficient of determination was greater than 50%, the correlation has been marked with an asterisk. Some of these many correlations are discussed individually below in the interpretation of morphological characters. Additional discussion of the methodological problem of which correlation coefficient is appropriate for use is found in Gatz (1975).

1. *Standard length* – Positive correlations: number of gill rakers. Negative correlations: *relative peduncle length; relative pectoral fin area.

2. *Pigmentation pattern* – No significant correlations.

3. *Completeness of lateral line* – Positive correlations: position of lateral line. No significant negative correlations.

4. *Position of lateral line* – Positive correlations: completeness of lateral line; aspect ratio of caudal fin; caudal span / body depth; number of caudal fin rays; position of pectoral fin; hypertrophy of pharyngeal teeth; percentage of red muscle. Negative correlations: pelvic fin aspect ratio; presence of jaw teeth; shape of jaw teeth; fine structure of gill rakers.

5. *Relative head length* – Positive correlations: *relative body depth; position of pectoral fin; position of pelvic fin; *width of mouth; *height of mouth; *presence of jaw teeth; *fine structure of gill rakers; number of pyloric caeca. Negative correlations: *caudal span / body

depth; *distance of pectoral fin from CG; position of dorsal fin; position of the mouth; hypertrophy of pharyngeal teeth.

6. *Flatness index* – Positive correlations: *relative body depth; *pelvic fin length, *relative eye size; protrusibility of the mouth. No significant negative correlations.

7. *Relative body depth* – Positive correlations: *relative head length; *flatness index; *pelvic fin length; *distance of pelvic fin from CG; relative eye size; protrusibility of the mouth. Negative correlations: *caudal span / body depth; distance of pectoral fin from CG.

8. *Index of trunk shape* – No significant correlations.

9. *Relative peduncle length* – No significant positive correlations. Negative correlations: *standard length; number of gill rakers.

10. *Caudal peduncle flatness index* – Positive correlations: relative size of forebrain. No significant negative correlations.

11. *Aspect ratio of caudal fin* – Positive correlations: position of lateral line; number of caudal fin rays; number of pectoral fin rays; position of pelvic fin; position of dorsal fin; hypertrophy of pharyngeal teeth; percentage of red muscle. Negative correlations: pelvic fin aspect ratio; position of jaw teeth.

12. *Caudal span / body depth* – Positive correlations: position of lateral line; number of caudal fin rays; distance of pectoral fin from CG; *position of pelvic fin, number of pelvic fin rays; *position of dorsal fin; *hypertrophy of pharyngeal teeth. Negative correlations: *relative head length; *relative body depth; pectoral fin length; position of pectoral fin; *pelvic fin length; *distance of pelvic fin from CG; *pelvic fin shape; *presence of jaw teeth; *fine structure of gill rakers.

13. *Number of caudal fin rays* – Positive correlations: position of lateral line; aspect ratio of caudal fin; caudal span / body depth; *position of pelvic fin; *number of pelvic fin rays; hypertrophy of pharyngeal teeth; percentage of red muscle. Negative correlations: position of pectoral fin; aspect ratio of pelvic fin; pelvic fin shape; relative size of optic lobes.

14. *Pectoral fin length* – Positive correlations: position of pectoral fin; *pelvic fin length; *distance of pelvic fin from CG; *pelvic fin shape; relative size of eye. Negative correlations: caudal span / body depth; pelvic fin position; *number of pelvic fin rays.

15. *Aspect ratio of the pectoral fin* – Positive correlations: pectoral fin shape. No significant negative correlations.

16. *Relative pectoral fin area* – No significant positive correlations. Negative correlations: standard length; *relative length of swim bladder.

17. *Distance of pectoral fin from center of gravity* – Positive correlations: caudal span / body depth; position of dorsal fin; hypertrophy of pharyngeal teeth. Negative correlations: *relative head length; *relative body depth; position of pectoral fin; *width of the mouth; presence of jaw teeth; number of pyloric caeca.

18. *Pectoral fin shape* – Positive correlations: pectoral fin aspect ratio. No significant negative correlations.

19. *Position of the pectoral fin* – Positive correlations: relative head length; caudal span / body depth; pectoral fin length; position of lateral line; pelvic fin length; pelvic fin aspect ratio; distance of pelvic fin from CG; pelvic fin shape; fine structure of gill rakers. Negative correlations: distance of pectoral fin from CG; number of caudal fin rays; *position of pelvic fin; *number of pelvic fin rays; percentage of red muscle.

20. *Number of pectoral fin rays* – Positive correlations: aspect ratio of caudal fin; position of the dorsal fin; hypertrophy of pharyngeal teeth. No significant negative correlations.

21. *Pelvic fin length* – Positive correlations: *flatness index; *relative body depth; *pectoral fin length; position of the pectoral fin; *distance of the pelvic fin from CG; pelvic fin shape; relative eye size; fine structure of gill rakers. Negative correlations: *caudal span / body depth;

position of the pelvic fin; number of pelvic fin rays; position of the dorsal fin.

22. *Aspect ratio of the pelvic fin* – Positive correlations: position of the pectoral fin; distance of pelvic fin from CG; pelvic fin shape; presence of jaw teeth; shape of jaw teeth; fine structure of gill rakers; *relative size of optic lobes. Negative correlations: position of the lateral line; aspect ratio of caudal fin; number of caudal fin rays; *position of pelvic fin; number of pelvic fin rays; hypertrophy of pharyngeal teeth; *percentage of red muscle; relative size of facial lobes.

23. *Relative pelvic fin area* – Positive correlations: shape of jaw teeth. No significant negative correlations.

24. *Distance of pelvic fin from center of gravity* – Positive correlations: relative head length; *relative body depth; *pectoral fin length; position of pectoral fin; *pelvic fin length, pelvic fin aspect ratio; *pelvic fin shape; *fine structure of gill rakers; number of pyloric caeca. Negative correlations: *caudal span / body depth; *position of pelvic fin; *number of pelvic fin rays; *position of dorsal fin.

25. *Pelvic fin shape* – Positive correlations: *pectoral fin length; position of pectoral fin; pelvic fin length; aspect ratio of pelvic fin; *distance of pelvic fin from CG; relative eye size; presence of jaw teeth; *fine structure of gill rakers; *relative size of optic lobes. Negative correlations; *caudal span / body depth; number of caudal fin rays; *number of pelvic fin rays: *position of pelvic fin; *position of dorsal fin; hypertrophy of pharyngeal teeth; percentage of red muscle; relative size of cerebellum; relative size of facial lobes.

26. *Position of pelvic fin* – Positive correlations: position of lateral line; aspect ratio of caudal fin; *caudal span / body depth; *number of pelvic fin rays; *position of dorsal fin; *hypertrophy of pharyngeal teeth; percentage of red muscle; relative size of facial lobes. Negative correlations: pectoral fin length; *position of pectoral fin; *aspect ratio of pelvic fin; *distance of pelvic fin from CG; *pelvic fin shape; presence of jaw teeth; shape of jaw teeth; relative size of optic lobes; pelvic fin length; *fine structure of gill rakers; number of pyloric caeca.

27. *Number of pelvic fin rays* – Positive correlations: caudal span / body depth; *number of caudal fin rays; *position of pelvic fin; position of dorsal fin; hypertrophy of pharyngeal teeth; relative size of facial lobes. Negative correlations: *pectoral fin length; *position of pectoral fin; pelvic fin length; aspect ratio of pelvic fin; *distance of pelvic fin from CG; *pelvic fin shape; relative eye size; presence of jaw teeth; fine structure of gill rakers; number of pyloric caeca; relative size of optic lobes.

28. *Position of dorsal fin* – Positive correlations: aspect ratio of caudal fin; caudal span / body depth; distance of pectoral fin from CG; number of pectoral fin rays; *position of pelvic fin; number of pelvic fin rays; *hypertrophy of pharyngeal teeth; percentage of red muscle. Negative correlations: relative head length; position of pectoral fin; pelvic fin length; *distance of pelvic fin from CG; *pelvic fin shape; *presence of jaw teeth; shape of jaw teeth; *fine structures of gill rakers; number of pyloric caeca.

29. *Relative eye size* – Positive correlations: *flatness index; relative body depth; pectoral fin length; pelvic fin length; protrusibility of the mouth. Negative correlations: number of pelvic fin rays; relative size of cerebellum.

30. *Position of the eyes* – No significant correlations.

31. *Eye pigmentation* – No significant positive correlations. Negative correlations: percentage of red muscle.

32. *Position of the mouth* – Positive correlations: *orientation of the mouth; *relative size of facial lobes. Negative correlations: relative head length; width of the mouth; *height of the mouth.

33. *Orientation of the mouth* – Positive correlations: *position of the mouth. Negative correlations: *height of the mouth.

34. *Relative width of the mouth* – Positive correlations: *relative head length;

*height of the mouth; presence of jaw teeth. Negative correlations: *distance of pectoral fin from CG; position of the mouth; hypertrophy of pharyngeal teeth.

35. *Relative height of the mouth* – Positive correlations: *relative head length; *width of the mouth. Negative correlations: *position of the mouth; orientation of the mouth.

36. *Protrusibility of the mouth* – Positive correlations: *flatness index; relative body depth; relative eye size; relative swim bladder volume. No significant negative correlations.

37. *Number of barbels* – Positive correlations: *relative size of forebrain; *relative size of cerebellum. No significant negative correlations.

38. *Number of branchiostegal rays* – Positive correlations: presence of jaw teeth; *shape of jaw teeth. Negative correlations: *hypertrophy of pharyngeal teeth; percentage of red muscle.

39. *Presence of jaw teeth* – Positive correlations: *relative head length; aspect ratio of pelvic fin; pelvic fin shape; width of the mouth; number of branchiostegal rays; *shape of jaw teeth; fine structure of gill rakers; number of pyloric caeca; relative size of optic lobes. Negative correlations: position of lateral line; *caudal span / body depth; distance of pectoral fin from CG; position of the pelvic fin; number of pelvic fin rays; *position of dorsal fin; *hypertrophy of pharyngeal teeth; percentage of red muscle.

40. *Shape of jaw teeth* – Positive correlations: relative head length; aspect ratio of pelvic fin relative pelvic fin area; *number of branchiostegal rays; *presence of jaw teeth; fine structure of gill rakers; relative size of optic lobes. Negative correlations: position of lateral line; aspect ratio of caudal fin; position of pelvic fin; position of dorsal fin; *hypertrophy of pharyngeal teeth; percentage of red muscle.

41. *Hypertrophy of pharyngeal teeth* – Positive correlations: position of lateral line; aspect ratio of caudal fin; *caudal span / body depth; number of caudal fin rays; distance of pectoral fin from CG; number of pectoral fin rays; *position of pelvic fin; number of pelvic fin rays; *position of dorasl fin; percentage of red muscle. Negative correlations: relative head length; aspect ratio of pelvic fin; pelvic fin shape; width of the mouth; *number of branchiostegal rays; *presence of jaw teeth; *shape of jaw teeth; fine structure of gill rakers; relative size of optic lobes.

42. *Shape of pharyngeal teeth* – No significant correlations.

43. *Number of gill rakers* – Positive correlations: standard length; fine structure of gill rakers. Negative correlations: relative peduncle length.

44. *Shape of gill rakers* – No significant correlations.

45. *Fine structure of gill rakers* – Positive correlations: relative head length; position of pectoral fin; distance of pelvic fin from CG; pelvic fin length; pelvic fin aspect ratio; pelvic fin shape; presence of jaw teeth; shape of jaw teeth; number of gill rakers; number of pyloric caeca; relative size of optic lobes. Negative correlations: position of lateral line; caudal span / body depth; position of pelvic fin; number of pelvic fin rays; position of dorsal fin; hypertrophy of pharyngeal teeth; percentage of red muscle; relative size of cerebellum; relative size of facial lobes.

46. *Relative volume of the swim bladder* – Positive correlations: *relative length of swim bladder. No significant negative correlations.

47. *Relative length of the swim bladder* – Positive correlations: *relative volume of swim bladder. Negative correlations: *relative pectoral fin area.

48. *Relative gut length* – No significant correlations.

49. *Number of pyloric caeca* – Positive correlations: relative head length; distance of pelvic fin from CG; presence of jaw teeth; fine structure of gill rakers. Negative correlations: distance of pectoral fin from CG; pelvic fin position; number of pelvic fin rays; position of dorsal fin.

50. *Percentage of red muscle in the peduncle* – Positive correlations: position

of lateral line; aspect ratio of caudal fin; number of caudal fin rays; position of pelvic fin; position of dorsal fin; hypertrophy of pharyngeal teeth. Negative correlations: position of pectoral fin; *aspect ratio of pelvic fin; pelvic fin shape; eye pigmentation; number of branchiostegal rays; presence of jaw teeth; shape of jaw teeth; fine structure of gill rakers; relative size of optic lobes.

51. *Relative size of the forebrain* — Positive correlations: caudal peduncle flatness index. No significant negative correlations.

52. *Relative size of the optic lobes* – Positive correlations: aspect ratio of pelvic fin; *pelvic fin shape; presence of jaw teeth; shape of jaw teeth; fine structure of gill rakers. Negative correlations: number of caudal fin rays; *position of pelvic fin; number of pelvic fin rays; hypertrophy of pharyngeal teeth; percentage of red muscle; relative size of cerebellum; relative size of facial lobes.

53. *Relative size of the cerebellum* – Positive correlations: *number of barbels; *relative size of vagal lobes; *relative size of facial lobes. Negative correlations: pelvic fin shape; relative eye size; fine structure of gill rakers; relative size of optic lobes.

54. *Relative size of the vagal lobes* – Positive correlations: *relative size of cerebellum. No significant negative correlations.

55. *Relative size of the facial lobes* – Positive correlations: position of pelvic fin; number of pelvic fin rays; *position of the mouth; relative size of cerebellum. Negative correlations: pelvic fin shape; aspect ratio of pelvic fin; fine structure of gill rakers; relative size of optic lobes.

56. *Relative size of the acoustic tubercles* – No significant correlations.

Factor Analysis.—Factor analysis of morphological characters was useful in pointing out some relationships not seen in the linear correlation analyses. Moreover, its basic property of ordering the importance of the covarying characters resulted in a ranking of trends which would not otherwise have been possible. The first three factors identify the three primary trends in the ecological differentiation among the fishes studied. These factors combine variables which relate to, respectively, technique of predation, maneuverability and utilization of habitats, and vertical zonation. These trends and all other trends defined by the factor analysis together with the associated resultant separations of species are described below. Altogether, the factor analysis indicated nine significant multivariate trends in the covariation of characters which jointly accounted for 79% of the total variance.

Factor 1, the major trend accounting for 31% of the character variance, indicated an association of several characters which relate to feeding behavior and technique. It indicates a positive association among having a high number of branchiostegal rays and the presence of jaw teeth (especially canines) and having many small teeth on the gill rakers; and a negative association of these characters with the presence of hypertrophied pharyngeal teeth and much red muscle in the peduncle. I interpret this to mean that the major morphological trend in ecological separation of the fishes studied has been in differentiation in feeding strategy between "lie-and-wait" biting predators (high scores on factor 1) and cruising suction feeders (low scores on factor 1). The ordination of families which results from consideration of this factor goes from Esocidae (pikes) with high factor scores through Percidae (perches), Ictaluridae (catfishes), and Centrarchidae (sunfishes) to Cyprinidae (minnows) with low scores (Fig. 1).

Factor 2 (12% variance) indicated the association among a number of characters relating to habitat separation by differences in body shape and proportions (see section on interpretation of morphological characters below). This factor associated a high ratio of caudal span to body depth, a large number of pelvic fin rays, and the location of both pelvic and dorsal fins entirely posterior to the center of gravity of the fish with low values for both the flatness index and relative body depth, short paired fins, pelvic fins which are rounded and located near the center of gravity of the fish and small relative eye size. Thus this factor separated the pickerel-like morphology at one extreme and the sunfish-like morphology at the other. Figure 2 shows the factor scores for the species on this factor.

Factor 3 (10% variance) identified characters associated with a benthic habit. Thus it associated large pectoral fin area with a small swim bladder and dorsally displaced eye position. Darters, naturally, showed especially high scores on this character (Fig. 3) and all suckers except *Erimyzon oblongus* showed somewhat positive scores. All other fishes showing positive scores on this factor I also infer to have a benthic preference (Fig. 3).

Factor 4 (7% variance) indicated the next most important trend in character variation among the fishes studied was that of being a small insectivore (see below). The major association shown by this factor was between small size and having a short relative gut length. To a lesser extent, these morphological features were also associated with presence of hooked pharyngeal teeth, few gill rakers, a supraterminal or terminal mouth which opens anteriorly, a long relative peduncle length and a large relative eye size. Fishes with high scores included both mid-water minnows and darters, *Gambusia affinis* and *Aphredoderus sayanus*; whereas sunfishes, pickerels, catfishes, and especially suckers had low scores (Fig. 4).

Factor 5 (6% variance) and Factor 6 (4% variance) each indicated associations of characters which differentiate two families. Factor 5 identified the relationship between having barbels, having a flattened peduncle and having few pectoral fin rays. All these characters are specializations of catfishes (Fig. 5). Factor 6 identified the association of large mouth size with large head size and having rounded pectoral fins placed near the center of gravity of the fish. Thus it identified a suite

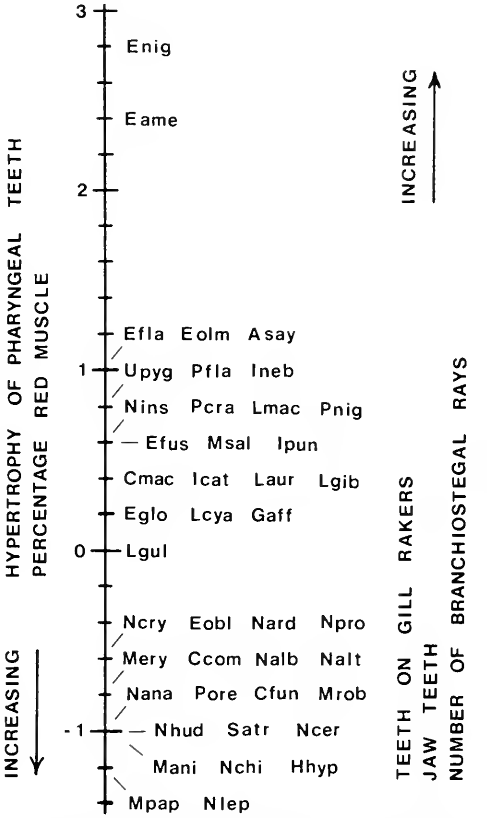

FIGURE 1. Ordination of species by mean factor scores on Factor 1 of the factor analysis of morphology. See text for interpretation. Abbreviations for species names are: Asay = *Aphredoderus sayanus*; Ccom = *Catostomus commersoni*; Cfun = *Clinostomus funduloides*; Cmac = *Centrarchus macropterus*; Eame = *Esox americanus*; Efla = *Etheostoma flabellare*; Efus = *Etheostoma fusiforme*; Eglo = *Enneacanthus gloriosus*; Enig = *Esox niger*; Eobl = *Erimyzon oblongus*; Eolm = *Etheostoma olmstedi*; Gaff = *Gambusia affinis*; Hhyp = *Hybopsis hypsinotus*; Icat = *Ictalurus catus*; Ineb = *Ictalurus nebulosus*; Ipun = *Ictalurus punctatus*; Laur = *Lepomis auritus*; Lcya = *Lepomis cyanellus*; Lgib = *Lepomis gibbosus*; Lgul = *Lepomis gulosus*; Lmac = *Lepomis macrochirus*; Mani = *Moxostoma anisurum*; Mery = *Moxostoma erythrurum*; Mpap = *Moxostoma pappillosum*; Mrob = *Moxostoma robustum*; Msal = *Micropterus salmoides*; Nalb = *Notropis alborus*; Nalt = *Notropis altipinnis*; Nana = *Notropis analostanus*; Nard = *Notropis ardens*; Ncer = *Notropis cerasinus*; Nchi = *Notropis chiliticus*; Ncry = *Notemigonus chrysoleucas*; Nhud = *Notropis hudsonius*; Nins = *Noturus insignis*; Nlep = *Nocomis leptocephalus*; Npro = *Notropis procne*; Pcra = *Percina crassa*; Pfla = *Perca flavescens*; Pnig = *Pomoxis nigromaculatus*; Pore = *Phoxinus oreas*; Satr = *Semotilus atromaculatus*; and Upyg = *Umbra pygmaea*.

of characters which indicate ecological specializations shared by most sunfishes and which differentiate them from the other fishes (Fig. 6).

The remaining three factors, together accounting for only 9% of the variance, did not in fact demonstrate clear cut morphological patterns. Factor 7 identified species which lack a lateral line canal (Fig. 7). Perhaps the most important point here is that although this character was assumed to indicate benthic habitat preferences (see below), the factor analysis did not associate it with the other characters in Factor 3. Factor 8 did not show any easily interpretable result but identified a weak association between small pelvic fin size and a low number of caudal fin rays (Fig. 8). Factor 9 identified species with extremely long, thin gill rakers (Fig. 9). There was also a tendency for a high index of trunk shape to be associated with this factor.

Gut Content Analysis. The results of the gut content analyses for the 33 common species are presented in Table 1 according to the coded format described previously. Notably, no two species were found to have the same diet in both size and composition. This result was obtained even with the relatively small sample size of individuals per species compared to most fish studies (e.g., Keast, 1966; Nilsson, 1960; Schwartz and Dutcher, 1962; although see also Carpenter, 1940) and the gross nature of the food categories. Dietetically, perhaps the two most similar

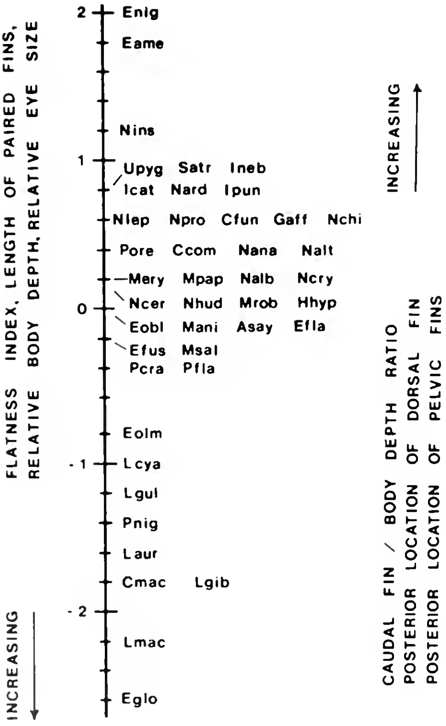

FIGURE 2. Ordination of species by mean factor scores on Factor 2 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

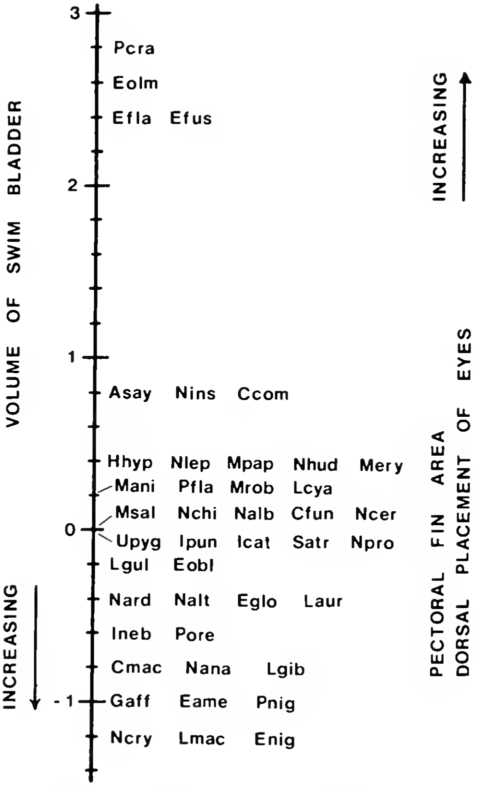

FIGURE 3. Ordination of species by mean factor scores on Factor 3 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

sympatric species were *Clinostomus funduloides* and *Semotilus atromaculatus*. Both of these species fed exclusively on terrestrial insects, but *Semotilus* took larger prey items in both relative and absolute terms. *Gambusia affinis* and *Notropis ardens* similarly differ only in prey size in this study, but were not found in the same stream.

A factor analysis with orthogonal rotation was performed on the food data in an effort to define trends in types of prey eaten. Nine factors accounting for 80% of the total variance were identified. The major trend (Factor 1 – 23% total variance) was one of prey size. Factor 1 separated predators on small items from those on large items, especially fish. Factor 2 (18% total variance) identified the second most important trend in feeding to be one relating to vertical position of prey. It separated bottom feeding as defined by the presence of ostracods, molluscs, filamentous algae and silt in the gut from surface feeding as defined primarily by eating terrestrial insects. All remaining factors merely identified individual food categories in order of their relative importance to numbers of species of fishes. Factor 3 (13% variance) identified the insects as the most important prey type and also indicated the tendency of fishes to eat either aquatic insects or terrestrial ones, but not both. Factor 4 (10% variance) related to

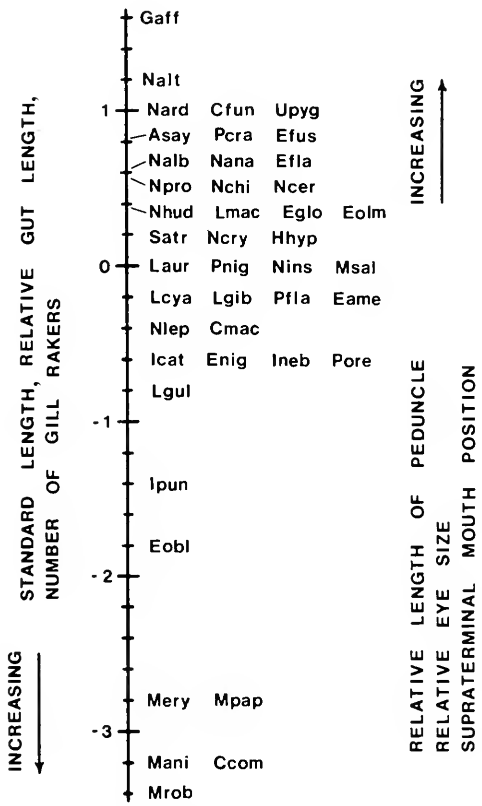

FIGURE 4. Ordination of species by mean factor scores on Factor 4 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

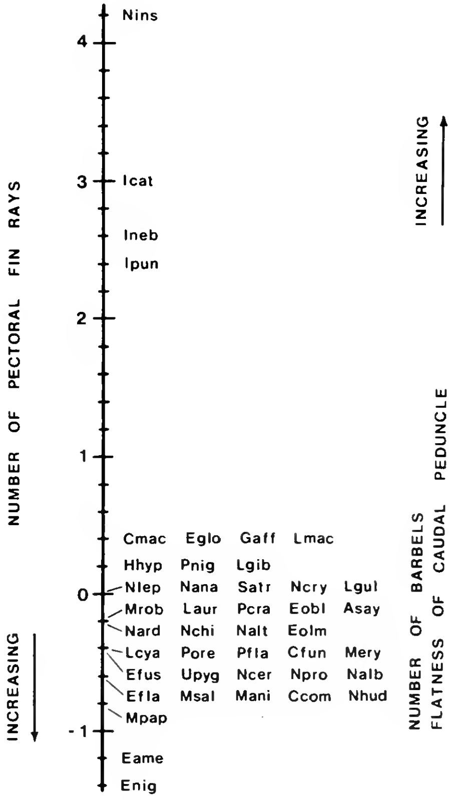

FIGURE 5. Ordination of species by mean factor scores on Factor 5 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

ship, could be demonstrated. Exceptions to this generalization are noted below where the characters are discussed seriatim. For each character the significance assumed at the outset, support from the literature, and the results of this study are given.

Superficial body and body shape characters

1. Standard length was assumed to be an indicator of prey size. Numerous studies of fish usually involving only a single species (e.g., Swynnerton and Worthington, 1940; Lindstrom, 1955 and references cited therein; Nilsson, 1955, 1958; Thomas, 1962; Hall *et al.*, 1970) have shown prey size to increase as a function of increase in body size. I found absolute prey size to be positively correlated (r = 0.690, $P < 0.001$) with standard length as was predicted. Relative prey size was not so correlated (r = 0.309, $0.10 > P > 0.05$). The correlation demonstrated here for this widely assumed relationship in ecological work (see Schoener and Gorman, 1968; Ashmole, 1968; Pianka, 1969; among others) is unusual in having been established for so broad a range of taxa.

2. Pigmentation pattern was assumed to indicate habitat and behavior according to the scheme of Nikolskii (1963). Nikolskii indicated the following correlates: (1)

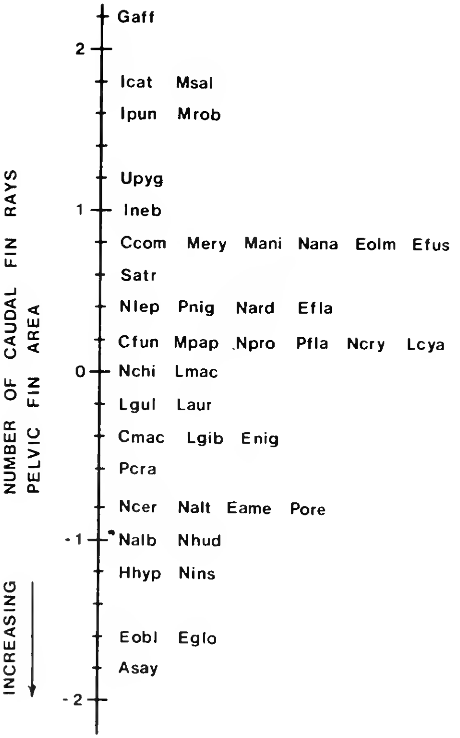

FIGURE 8. Ordination of species by mean factor scores on Factor 8 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

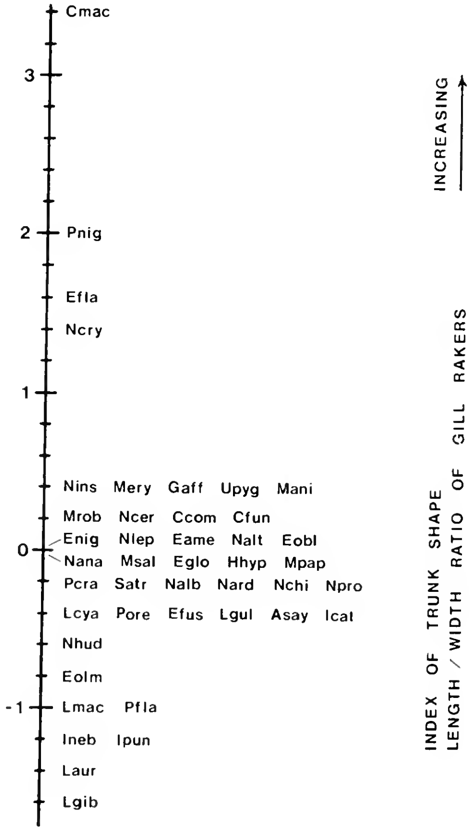

FIGURE 9. Ordination of species by mean factor scores on Factor 9 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

eating copepods; Factor 5 (8%), diatoms; Factor 6 (6%), terrestrial invertebrates; Factor 7(5%), amphipods and isopods; Factor 8 (4%), filamentous algae; and Factor 9 (3%), crayfish.

The results of the gut content analyses for the rare species according to decreasing order of importance of categories present are: *Anguilla rostrata* – empty; *Umbra pygmaea* – aquatic insects; *Notropis hudsonius* – aquatic insects, silt; *Moxostoma anisurum* – aquatic insects, molluscs, ostracods, copepods, and silt; *M. erythrurum* – aquatic insects, ostracods, diatoms, silt and sand; *M. pappillosum* – ostracods, vascular plants, silt; *M. robustum* – aquatic insects, sand; *Ictalurus catus* – terrestrial insects, sand (gut nearly empty); *I. punctatus* – crayfish, aquatic insects, terrestrial insects, vascular plants; *Enneacanthus gloriosus* – aquatic insects, terrestrial insects; and *Percina crassa* – aquatic insects and sand.

These results were utilized below in the interpretation of the morphological characters.

Interpretation of Morphological Characters.—The initial choice of all characters was based on some inferred functional and/or ecological significance. Although in most cases there was some precedent in the literature for the supposed association between character and function, the experimental substantiation of any particular association has been extremely rare. In fact, seldom have data been compiled (but see Aleev, 1969) so that even a statistical correlation, let alone a causal relation-

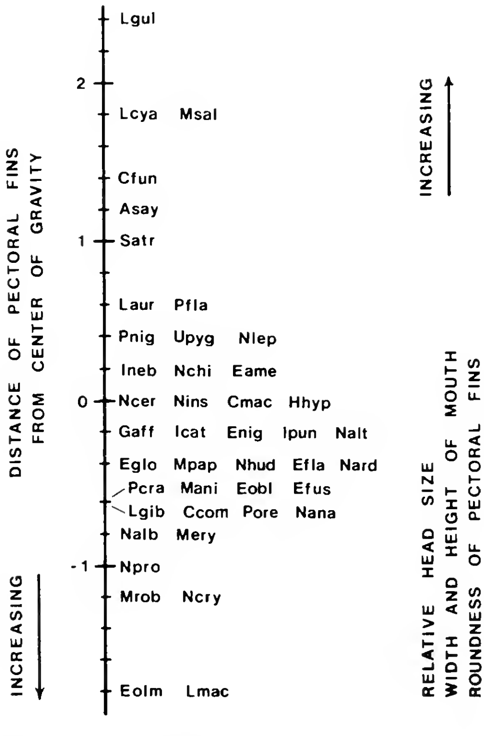

FIGURE 6. Ordination of species by mean factor scores on Factor 6 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

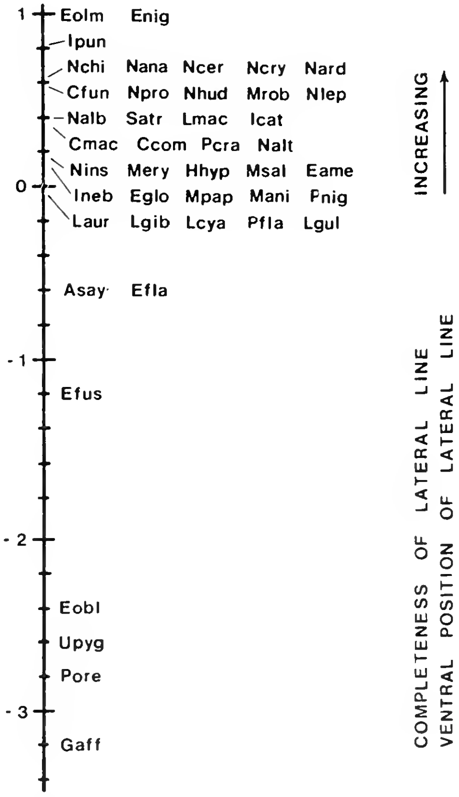

FIGURE 7. Ordination of species by mean factor scores on Factor 7 of the factor analysis of morphology. See text for interpretation. Abbreviations as in legend for Fig. 1.

silvery or reflective sides – solitary pelagic; (2) countershading with a dark lateral band – schooling pelagic; (3) mottled pattern or vertical bars – vegetal or benthic rocks; and (4) countershading without either silveriness or a lateral band – benthic over a sand bottom.

3. Completeness of the lateral line canal was assumed to be an indicator of habitat and behavior also. This sensory structure which detects water movements tends to be best developed in active fishes and reduced or absent in bottom dwellers and sluggish forms (Branson and Moore, 1962).

4. The position of the lateral line canal was assumed to relate to vertical habitat position and to the predation relations of the fish. The character states used and the particular associations were: (0) lacking – benthic or sluggish forms; (1) curving dorsally – fishes which have predators and/or prey dorsal to them in the water column; (2) horizontal – predators in the upper and midwater region; and (3) curving ventrally – fishes which feed high in the water column and are subject to predation from below (Marshall, 1971; Disler, 1971).

5. Relative head length was assumed to be related to prey size, a fish with a relatively larger head being able to handle relatively larger prey. To the best of my knowledge this relationship has not previously been studied in fishes, although Schoener (1968) has demonstrated it to hold for certain lizards. My results show that both absolute ($r = 0.697$, $P < 0.001$) and relative ($r = 0.701$, $P < 0.001$) prey size are positively correlated with relative head length. Thus, large headed little fish like *Aphredoderus sayanus* took large prey. Both relative head length and standard length are shown in this study to be equally good predictors of absolute prey size, but only the former seems strongly related to relative prey size.

6. Flatness index was assumed to indicate habitat water velocity with a lower index being associated with more rapidly flowing water (H.E. Evans, 1950; Hora, 1922; Nikolskii, 1933). As noted above, this character and the next showed a significant positive correlation with each other as well as being associated in the factor analysis (Factor 2, Fig. 2). Both of these results should be expected given the predicted common dependence of these characters on habitat water velocity.

7. Relative body depth was assumed to be inversely related to habitat water velocity and directly related to capacity for making vertical turns, i.e., about the axis of pitch (Nikolskii, 1933; Aleev, 1969). Significant differences in relative body depth were found between samples of each of three species of centrarchids collected in two different streams (Table 2). For two of the species, an increased sample size was employed to guard against the possibility of a non-random error in the initial measurement or sampling which involved only ten individuals.

The intraspecific differences would support the proposed interpretation if (1) habitat water velocity were higher in East Prong Little Yadkin (Pee Dee) than in Maho Creek (Roanoke) and higher in the latter than in Mud Creek (Cape Fear); and (2) the morphological variation were due to adaptation to these local physical conditions. The required differences in habitat water velocities seem likely. East Prong Little Yadkin has a gradient three to four times greater than the other two streams and hence would be expected to have a mean velocity one and a half to two times greater than either of the others (Hynes, 1970). The few pools which are present are small and isolated backwaters are virtually nonexistent. Thus likely both *Lepomis auritus* and *Lepomis cyanellus* are subjected to a stronger selective pressure for increased tolerance to flowing water in East Prong Little Yadkin than in Maho Creek. Alternative possibilities, e.g., character displacement, or in the case of the introduced *L. cyanellus*, founder effect, do exist, but seem less likely. With regard to the comparison of *Pomoxis nigromaculatus* in the two streams, a higher mean velocity is expected in Maho Creek than in Mud Creek because although the

TABLE 1. Results of the gut content analyses for the 33 common species of fishes. The numerical entries in the table for each food category are character codes for, respectively, frequency and importance of that particular prey type in the diet of the species. For a complete explanation of the coding , see the methods section of the text.

	Fish	Copepods	Ostracods	Aquatic insects	Terrestrial insects	Crayfish	Amphipods and isopods	Diatoms	Filamentous algae	Molluscs	Sand	Silt	Terrestrial inverts	Vascular plants	Absolute prey size	Relative prey size
Esox americanus	23	11	11	23	22	55	1	11	11	1	1	1	22	1	4	4
Esox niger	55	22	11	33	11	33	1	11	11	1	1	1	22	1	6	5
Clinostomus funduloides	11	11	11	11	66	11	1	11	11	1	1	1	11	1	2	2
Hybopsis hypsinotus	11	23	11	55	23	22	1	22	11	1	1	5	11	1	1	2
Nocomis leptocephalus	11	11	11	45	23	23	1	23	11	1	4	1	11	1	2	2
Notemigonus crysoleucas	11	22	11	33	34	11	1	44	23	1	2	4	11	1	1	1
Notropis alborus	11	11	11	33	23	11	1	34	11	1	1	3	11	1	1	1
Notropis altipinnis	11	11	11	11	55	11	1	11	33	1	1	1	11	1	1	2
Notropis analostanus	11	11	11	33	55	11	1	22	23	1	1	2	11	1	1	2
Notropis ardens	11	11	11	33	55	11	1	11	11	1	1	1	11	1	2	2
Notropis cerasinus	11	11	11	65	43	11	1	11	22	1	1	3	11	1	3	3
Notropis chiliticus	11	11	11	33	45	11	1	11	33	1	2	1	11	1	2	2
Notropis procne	11	11	11	44	22	11	1	44	22	1	1	4	11	1	1	1
Phoxinus oreas	11	11	11	23	11	11	1	65	11	1	1	6	11	1	1	1
Semotilus atromaculatus	11	11	11	11	66	11	1	11	11	1	1	1	11	1	3	4
Catostomus commersoni	22	11	32	65	23	32	1	11	33	1	6	3	23	1	3	2
Erimyzon oblongus	11	44	33	43	11	11	1	23	32	1	2	6	22	1	1	1
Ictalurus nebulosus	11	11	44	33	11	22	1	11	33	2	3	5	11	2	2	1
Noturus insignis	11	11	11	65	22	11	1	11	11	1	6	1	11	1	2	1
Aphredoderus sayanus	11	11	11	55	11	11	2	11	11	1	2	2	23	1	3	6
Gambusia affinis	11	11	11	33	55	11	1	11	11	1	1	1	11	1	1	1
Centrarchus macropterus	23	23	11	43	44	11	1	11	11	1	1	1	11	1	3	3
Lepomis auritus	11	11	11	54	33	33	1	11	11	1	1	1	23	2	4	4
Lepomis cyanellus	11	11	11	43	33	44	2	11	11	1	1	2	11	1	4	5
Lepomis gibbosus	11	11	33	56	43	11	1	11	22	1	1	4	11	1	2	2
Lepomis gulosus	11	11	11	44	43	33	1	11	11	1	1	1	11	1	4	5
Lepomis macrochirus	11	22	11	55	43	11	1	11	11	1	1	2	11	1	2	2
Micropterus salmoides	33	11	11	23	44	23	1	11	11	1	1	1	11	1	3	4
Pomoxis nigromaculatus	33	22	11	11	65	33	1	11	11	1	1	1	22	1	3	2
Etheostoma flabellare	11	11	11	65	11	11	1	11	11	1	1	1	22	1	2	3
Etheostoma fusiforme	11	43	11	65	11	11	1	11	11	1	1	1	11	1	1	2
Etheostoma olmstedi	11	11	11	65	11	11	1	11	11	1	3	1	11	1	1	2
Perca flavescens	11	11	11	65	11	33	1	11	11	1	1	1	11	1	2	2

TABLE 2. Intraspecific variation in relative body depth (see text for definition) in three species of centrarchids. NM= not measured.

Species	n	East Prong	Mud Cr.	Maho Cr.	F value	Signif.
Lepomis auritus	15	0.397	NM	0.444	9.806	< 0.01
Lepomis cyanellus	10	0.379	NM	0.395	5.804	< 0.05
Pomoxis nigromaculatus	28	NM	0.431	0.403	8.874	< 0.01

gradients are similar in both, the former is larger (Hynes, 1970). Again, the observed differences correspond to the hypothesized interpretation of the character. No other species was found to show intraspecific variation in this character. Such variation has been reported in Gromov (1973) who compared lake and river populations of carp.

8. Index of trunk shape was assumed to be directly related to hydrodynamic ability in that a high value is associated with a late separation of the boundary layer (Aleev, 1969; Ovchinnikov, 1971). Hence higher values are assumed to indicate fishes which spend more time cruising. However, Aleev (1969, Table 21) did point out that body height affects the index so that deep bodied fishes are apt to have higher values than one might expect from their swimming habits.

My results tend to substantiate Aleev's findings. In the first place, I did not find this character to show a significant correlation with any other. Inasmuch as other characters were also assumed to relate to various aspects of hydrodynamics and cruising, this suggests either that this character measures some unique aspect of swimming ability, or that there are other irregularities in the values. The ordination of species means for this character suggests the latter to be the case as high values are recorded both for cruising minnows and for several species of laterally flattened, deep bodied centrarchids. Thus my results indicate the same ambiguity in the significance of this index as those of Aleev (1969).

9. Relative peduncle length was assumed to be directly related to swimming ability (Hora, 1922; Kanep, 1971).

10. Caudal peduncle flatness index was assumed to relate inversely to amplitude of swimming movements (Nursall, 1958) and, like flatness index of the body, to be higher in less active swimmers. In general, a listing of species according to increasing value for this character produced an ordination of species which, based on literature description of their habits, would be concordant with the assumed significance. Thus, for example, *Pomoxis nigromaculatus* showed a higher index than *Lepomis auritus* and *L. cyanellus* which in turn showed higher values than *Micropterus salmoides*.

Caudal fin characters

11. Aspect ratio of the caudal fin was assumed to be directly proportional to the amount of swimming the fish does (Nichols, 1915; Harris, 1953; Nursall, 1958; Aleev, 1969; Kramer, 1960). The positive correlation of this character with the percentage of red muscle in the peduncle is the most tangible evidence for the assumed function (see discussion of red muscle, below).

12. Caudal span/body depth ratio was assumed to be directly proportional to speed of swimming in that ratios of increasing magnitude greater than one indicate better hydrodynamics for the caudal fin as the lobes of the fin are out of the zone of vortices shed from the body (Aleev, 1969). I found low values for sunfishes and high values for minnows which, according to the hydrodynamic argument

presented above, would imply that minnows are faster swimmers than sunfishes. Experimental substantiation of this is lacking.

13. The number of caudal fin rays was assumed to be directly proportional to the significance of the caudal fin as the principal means of locomotion (Marshall, 1971). My results suggest the separations of species given by this character may well be more phylogenetic than functional or ecological for my species. For instance, all sunfishes had 17 caudal fin rays, suckers had 18, and both minnows and pickerels had 19.

Paired fin characters

Although the importance of the paired fins in low speed maneuvering has been investigated by a number of persons (e.g., Aleev, 1969; Breder, 1926; Gosline, 1971; Gray, 1968; Harris, 1953), precise associations between functional specializations and particular morphological features have not always been defined. Thus for some of the following characters, no definite functional correlate is given but rather an assumed function based on theoretical considerations.

14. Pectoral fin length was assumed to increase as a function of amount of low speed maneuvering in the behavior of the fish (Gray, 1968; Starck and Schroeder, 1970; Kanep, 1971). Factor 2 of the factor analysis indicates an association between high values in this character and body shape characters which indicate low habitat water velocity (see Fig. 2). One might expect a fish in quiet water to do more low speed maneuvering than one living in fast water.

15. Aspect ratio of the pectoral fin was assumed likely to relate in some manner to the ways the fin might be able to function. The only correlation found for this character was with the next.

16. Relative pectoral fin area was assumed to be directly proportional to the capacity of the fin to function in braking, fanning to maintain position, and acceleration from the stop (Gosline, 1971). My results, particularly Factor 3 of the factor analysis (Fig. 3), indicate large relative pectoral fin area is also associated with benthic habits. Recently, A.N. Jones (1975) also reported pectoral fin area to relate to benthic living, particularly in areas of current. Jones found that salmon had larger pectoral fins than trout and were more frequently found in riffles. He suggested that the larger pectoral fin of the salmon enables it to "hold station" in riffles by deflecting water over the fin and thereby enable salmon to occupy territories unavailable to trout. Keenleyside (1962) reported observations made while skin diving which confirm this interpretation. He observed that salmon rest on the bottom with their pectoral fins spread, whereas trout do not maintain contact with the bottom, but rather usually swim actively against the current to maintain position. For additional information, see also Lundberg and Marsh (1976) who discuss how suckers use their pectoral fins on the substrate.

17. Relative distance of the pectoral fin from the center of gravity of the fish was assumed to be directly proportional to the importance of the pectoral fin in the turning and maneuverability of the fish (Aleev, 1969; Breder, 1926) in that all else being equal, a larger distance from the center of gravity provides greater torque. The various correlations reported above for this character do not provide any real support for this argument.

18. Pectoral fin shape, like its aspect ratio, was assumed to relate to its function. One correlate in the literature is that rounded fins are characteristic of fishes which remain motionless in midwater (Aleev, 1969).

19. Position of the pectoral fin relative to the center of gravity was assumed to have something to do with the turning capacity of the fish.

20. Number of pectoral fin rays has been suggested by Hubbs (1941) to be directly proportional to the amount of time the fish spends in the current.

21. Pelvic fin length was assumed to be related to habitat preference, being longer

in rocky habitat species and shorter in free swimming species (Starck and Schroeder, 1970).

22. Aspect ratio of the pelvic fin was assumed to be small in fishes in which the pelvic fin is used only for a brake or forward swimming aid and large if the fins are important for backing and hovering (Harris, 1937).

23. Relative pelvic fin area was assumed to be largest in fishes with demersal habitat preference (Aleev, 1969).

24. Relative distance of the pelvic fin from the center of gravity of the fish was assumed to be an indication of torque and hence of the importance of the pelvic fin in the turning and maneuverability of the fish (Aleev, 1969; Breder, 1926).

25. Pelvic fin shape was assumed to relate to its function. One correlate in the literature is that more falcate pelvic fins are found in fishes which are constantly in the current (Hubbs, 1941).

26. Position of the pelvic fin relative to the center of gravity was assumed to lower with increased proportional use of the pectoral fin as brakes because the pelvics must be close to the center of gravity to counteract the pitch induced by such braking (Harris, 1938). Values were assumed to be higher with increased importance of the pelvic fins in turning movements (Breder, 1926).

27. Number of pelvic fin rays was assumed to be directly proportional to the amount of time the fish spends in the current (Hubbs, 1941).

28. Position of the dorsal fin relative to the center of gravity was assumed to reflect what functions the dorsal fin was capable of performing: (a) anterior rudder function is better the further anterior to the center of gravity the fin is, (b) keel function is best served at the level of the center of gravity, (c) stabilization of forward movement is associated with a posterior position, and (d) posterior rudder and/or locomotory function are best performed the further posterior the fin is positioned (Gosline, 1971).

Head characters

29. Relative eye size was assumed to be directly proportional to the development of visual capabilities in the fish (Protasov, 1970) and hence this character was assumed directly proportional to the importance of sight in the feeding of the fish (H.E. Evans, 1950).

Not all species reputed to be visual predators, e.g., *Esox niger*, had large relative eye sizes. Part of the explanation for this might be the known negative allometry of eye size in fishes (Martin, 1949). A transformation based on regressions of absolute eye size on standard length and using the intercepts as a measure of relative eye size merely gave a second value nearly perfectly correlated ($r = 0.9985$) with the original character.

Somewhat more disconcerting than the partially counterintuitive sequencing of some species in values for relative eye size was the low correlation of this character with relative size of the optic lobes, which was also assumed to be directly proportional to the development of visual capabilities in the fish. The Pearson coefficient was 0.455 ($0.01 > P > 0.005$) and the Spearman, 0.476 ($P = 0.005$). Still, enough of a trend appeared to be evident between visual habits of well known species and the relative eye size values for me to consider the use of this character to be valid.

30. Position of the eyes was assumed to relate to vertical habitat preference. Lateral placement was assumed to indicate pelagic habit and increased displacement dorsally was associated with the assumption of a more sedentary mode of life (Aleev, 1969). My results provide support for this interpretation. Although no significant simple correlations with this character were identified, the factor analysis (Factor 3, Fig. 3) did indicate it to be associated with several other characters which also were assumed to reflect benthic habitat preference.

31. Eye pigmentation was assumed to reflect habitat and behavior. The assumed correlates were: no pigmentation – slow

moving and/or benthic fishes; horizontal line of pigmentation – cruising habit; vertical line through the eye – fast turning habit; and presence of both a horizontal and a vertical line through the eye – both specializations (Barlow, 1972).

32. Position of the mouth was assumed to indicate the location of the food eaten relative to the fish (Aleev, 1969; Al-Hussaini, 1949; Schmitz and Baker, 1969). Schutz and Northcote (1972) provided experimental support for this interpretation. They found that Dolly Varden (*Salvelinus malma*) which have subterminal mouths were more effective bottom feeders than cutthroat trout (*Salmo clarki clarki*) which have terminal mouths and vice versa when both species were tested in aquaria. This evidence, notably, is only for two closely related species. My results which support the assumed interpretation are discussed below in conjunction with orientation of the mouth.

33. Orientation of the mouth was also assumed to indicate from where in the habitat a fish obtained its foods. Given that certain types of prey are apt to be found on or near the bottom (e.g., ostracods, diatoms, aquatic insect larvae) and others only at the surface or in mid-water (e.g., water striders, terrestrial insects, fishes), the existence of correlations between those types in the gut and mouth position and/or orientation can be determined. Due to the manner in which I coded position of the mouth and orientation of the mouth, one should expect positive correlations between these characters and items of benthic prey and negative correlations with surface and mid-water prey.

Table 3 shows the correlations for all prey categories with these two morphological features. The expected relations, although weak, do hold for ostracods, filamentous algae, aquatic insects and frequency of terrestrial insects. They were not demonstrated for diatoms or for fishes. The strongest positive correlations were with sand and silt, and the strongest negative, with prey size. The former cor-

TABLE 3. Correlations of gut contents with position and orientation of the mouth. The first figures for each category present coefficient and significance for frequency. The second figures give coefficient and significance for importance, where applicable (see text).

Gut content category	Correlations with position of the mouth		Correlations with orientation of the mouth	
Fish	-.31, NS	-.35, $P < .05$	-.24, NS	-.28, NS
Copepods	+.18, NS	+.17, NS	+.06, NS	+.02, NS
Ostracods	+.39, $P < .05$	+.31, NS	+.46, $P < .01$	+.38, $P < .05$
Aquatic insects	+.39, $P < .05$	+.40, $P < .02$	+.45, $P < .01$	+.47, $P < .01$
Terrestrial insects	-.43, $P < .02$	-.29, NS	-.44, $P < .01$	-.34, NS
Crayfish	-.29, NS	-.37, $P < .05$	-.15, NS	-.22, NS
Amphipods and isopods	-.28, NS		-.23, NS	
Diatoms	+.28, NS	+.34, NS	+.25, NS	+.30, NS
Filamentous algae	+.45, $P < .01$	+.38, $P < .05$	+.46, $P < .01$	+.40, $P < .05$
Molluscs	+.12, NS		+.15, NS	
Sand	+.63, $P < .001$		+.54, $P < .002$	
Silt	+.47, $P < .01$		+.48, $P < .005$	
Terrestrial invertebrates	-.12, NS	-.07, NS	-.14, NS	-.06, NS
Vascular plants	-.05, NS		-.01, NS	
Absolute prey size	-.55, $P < .001$		-.41, $P < .02$	
Relative prey size	-.60, $P < .001$		-.52, $P < .002$	

relations are considered very strong evidence that fishes with more ventral mouths obtain their prey from the bottom and those with more terminal or anterior mouths do not. The negative prey size correlation also supports the assumed significance of these characters in that the smallest prey items in this study, diatoms, tend to be benthic organisms in lotic habitats. Thus, my results indicate support for the hypothesized significances for both of these characters for a wide range of taxa.

34. Relative width of the mouth was assumed to be directly proportional to the size of food eaten (Aleev, 1969; Forbes and Richardson, 1920; Starck and Schroeder, 1970). My results pertaining to this character are discussed below with those for the next character.

35. Relative height of the mouth was also assumed to indicate size of prey. This is another of the few characters I used for which direct experimental evidence exists (Werner, 1974). Werner showed that optimal prey size for *Lepomis cyanellus* and *L. macrochirus* was a function of mouth size. My results show that both width and height of the mouth are highly significantly correlated with both relative and absolute prey size (for both Spearman and Pearson coefficients, all r's are between 0.594 and 0.681; all P's are less than 0.001). Thus my correlative evidence supports my having assumed generality of the type results obtained by Werner (op. cit.). Additionally, my extensive multifamily correlations also indicate that the correlations of prey size with gape (of the mouth) found by Thomas (1962) for two salmonids and Northcote (1954) for two cottids were not unique to these two families.

36. The index of protrusion was assumed to be greatest in fishes with the smallest prey. This is based on the assumption that strength of bite is inversely related to the degree to which the premaxillary is protruded and that a stronger bite is required to capture a large item of prey than a small one (Al-Hussaini, 1949; Aleev, 1969; Gosline, 1973).

My results do not support these assumptions. This index did not correlate negatively with either relative or absolute prey size ($r = -0.14$) among all species of fishes as should have been predicted. Five of the eight species taking prey of the largest relative prey sizes (*Esox niger, E. americanus, Aphredoderus sayanus, Semotilus atromaculatus,* and *Micropterus salmoides*) did have mouths with an index of protrusion of one or nearly one (i.e., no or very little protrusibility); however, so did such fishes as all members of the genera *Etheostoma* (darters) and *Ictalurus* (catfishes) which take prey of very small relative size. The other three predators on large relative size prey (*Lepomis auritus, L. cyanellus*, and *L. gulosus*) all had mouths which showed high values for this index. This character therefore seems to be of limited usefulness in comparing fishes between different families.

37. Number of barbels was assumed to be directly proportional to the importance of non-optic senses in feeding (Gilbert and Bailey, 1972) and the benthic habit of the fish (Gosline, 1973; Aleev, 1969). The barbels are innervated by the facial nerve so that one should expect this character to be strongly correlated with the relative size of the facial lobes. In fact, only the Pearson correlation of these two variables was significant ($r = 0.790$, $P < 0.001$) and not the Spearman.

38-40. Number of branchiostegal rays, presence of jaw teeth, and shape of jaw teeth were all assumed to be inversely related to the importance of suction in the capture of prey (Gosline, 1973). In addition, shape of jaw teeth was assumed to indicate size of prey.

One would not expect suction to be important in the capture of large prey, i.e., such items as fish or crayfish. In view of this expectation, the positive correlations of absolute prey size with number of branchiostegal rays ($P \le 0.001$), with presence of jaw teeth ($P < 0.002$) and with the shape of jaw teeth ($P < 0.002$) provide evidence in support of the function I assumed for these characters. Additionally, my results provide further support for this proposed functional significance in that all three characters showed positive correlations with both frequency and importance of fish and crayfish (P's < 0.05 to < 0.001).

41. Hypertrophy of teeth on the pharyngeal arches was assumed to relate to manner of feeding, especially to be directly related to the importance of suction in capture of prey (Gosline, 1973). My results support this hypothesis in that a negative correlation was found between absolute prey size and this character ($P < 0.02$).

42. Shape of pharyngeal teeth was assumed to relate to dominant food type in the diet (H.E. Evans, 1950; Al-Hussaini, 1949). I found a weak positive correlation ($P < 0.05$) of the character with the frequency of occurrence of both filamentous algae and ostracods in the diet (recall the coding for this character provided a high value for teeth with grinding surfaces). No further significant correlations were determined. Apparently many different fish species, each with its own type of dentition, are able to eat from the same broad prey categories used in this study.

43. Number of gill rakers was assumed to be inversely correlated with the presence of larger and more benthic prey in the diet (Kliewer, 1970; Himberg, 1970; Nilsson, 1958). My results did not support a generalization of this observation on salmonids; in fact, they show the reverse relationship. Absolute prey size and number of gill rakers gave a positive correlation ($r = 0.519$; $P < 0.002$). Several factors enter into this: (1) considering the many reduced plates in *Esox* each to represent a gill raker so that those predators on large prey have among the highest gill raker counts; (2) the generally high gill raker counts among sunfishes; and (3) the generally low gill raker counts among minnows. Thus a strong taxonomic component negates the general utility of this character along lines such as those demonstrated by Kliewer (1970) and Himberg (1970).

In this study I varied my interpretation of the number of gill rakers depending on the degree of taxonomic relatedness of the species being compared. For intrafamilial comparisons, I assumed that the usual functional interpretation is correct and that a low number of gill rakers was indicative of large benthic prey. For general interfamilial comparisons, I interpreted differences in number of gill rakers by bearing in mind that the two strongest positive correlations with this character for all species are with items of the two largest prey size categories in the diet: (1) fish ($P < 0.001$) and (2) crayfish ($P < 0.01$). <

44. Shape of the middle gill raker, as measured by the ratio of length to width, was assumed to be inversely related to food size (Kliewer, 1970; Starck and Schroeder, 1970; Forbes and Richardson, 1920). My results lend little support to this assumption. No correlation between this variable and food size was found. Nor was this character correlated with any of the other morphological characters. The only correlation found was a weak positive association between shape of gill rakers (high values indicate long, thin gill rakers) and importance of copepods in the diet ($r = 0.373$, $P < 0.05$). This gives minor support to the functional interpretation assumed in this study, but obviously more parameters are operational in the selective regime for this feature than just the ability to obtain small mobile prey like copepods.

45. Finer structure of the gill rakers was assumed to relate to food type and food handling. My results supported this assumption as a number of significant relationships between prey and gill raker armament were observed. The strongest of these correlations are with prey size. High numbers of fine teeth on the gill rakers are correlated both with absolute size of prey ($r = 0.577$; $P < 0.001$) and relative size of prey ($r = 0.613$; $P < 0.001$). Weaker correlations were observed with individual categories of large prey types: crayfish ($r = 0.51$; $P < 0.002$); fish ($r = 0.42$; $P <$

0.02); and non-insect terrestrial invertebrates (r = 0.39; $P < 0.05$). Weak negative correlations were found with both diatoms (r = -0.42; $P < 0.02$) and filamentous algae (r = -0.41; $P < 0.05$), which indicated a tendency for fishes eating these latter two types of prey to have smooth or ridged gill rakers.

Internal body characters

46. Relative volume of the swim bladder was assumed to be inversely proportional to the bottom dwelling preference of the fish (Forbes, 1880; Bridge and Haddon, 1889) and also negatively correlated with water speed in the habitat of the fish (Hora, 1922; Gee, 1968, 1974). This latter relationship is one of the very few in which experimental evidence exists that demonstrates a causal relationship between ecological conditions and morphology. Gee (1970, 1972) and Gee et al. (1974) have presented data that indicate a number of species of fishes respond to an increase in water velocity in the laboratory by decreasing the volume of their swim bladders.

A complete listing of relative volume of the swim bladder (first value) and relative length of the swim bladder (second value) follows. Species are listed in order of increasing swim bladder volume and parentheses around a species name and values indicates that the sample size was 1 or 2 rather than the usual 10. The species mean values are: *Etheostoma flabellare* 0,0; *E. fusiforme* 0,0; *E. olmstedi* 0,0; (*Percina crassa* 0,0); *Aphredoderus sayanus* 0.036,0.282; (*Anguilla rostrata* 0.037, 0.200); (*Umbra pygmaea* 0.38,0.359); *Noturus insignis* 0.046,0.098; *Notropis chiliticus* 0.054,0.318; (*Notropis hudsonius* 0.054,0.341); (*Moxostoma robustum* 0.054,0.462); (*Ictalurus punctatus* 0.054, 0.182); *Nocomis leptocephalus* 0.056, 0.304; *Notropis ardens* 0.056,0.311; *Catostomus commersoni* 0.057,0.360; *Clinostomus funduloides* 0.061,0.340; *Perca flavescens* 0.061,0.330; *Erimyzon oblongus* 0.061,0.358; *Lepomis cyanellus* 0.061, 0.297; *Notropis procne* 0.062,0.321; *Semotilus atromaculatus* 0.063,0.344; *Notropis cerasinus* 0.064,0.363; (*Ictalurus catus* 0.065,0.186); *Ictalurus nebulosus* 0.066,0.197; *Esox niger* 0.067,0.415; *Micropterus salmoides* 0.068,0.314; *Phoxinus oreas* 0.068,0.336; *Hybopsis hypsinotus* 0.068,0.343; *Notropis analostanus* 0.069, 0.356; (*Enneacanthus gloriosus* 0.071, 0.343); *Lepomis gibbosus* 0.071,0.336; *Lepomis auritus* 0.072,0.315; *Gambusia affinis* 0.074,0.264; *Notropis altipinnis* 0.074,0.341; (*Moxostoma erythrurum* 0.075,0.473); *Moxostoma anisurum* 0.076,0.446; *Lepomis gulosus* 0.076, 0.341; *Notropis alborus* 0.078, 0.337; *Centrarchus macropterus* 0.079,0.426; *Lepomis macrochirus* 0.080,0.346; (*Moxostoma pappillosum* 0.083,0.465); *Esox americanus* 0.083,0.435; *Notemigonus crysoleucas* 0.083,0.378; *Pomoxis nigromaculatus* 0.085,0.364.

A comparison of habitat observations of the fishes with the values obtained in this study confirmed both of the points in the assumed significance of this variable. Known bottom dwellers in fast current regions had small swim bladder volumes. For example, all *Etheostoma* studied lacked gas-filled swim bladders and the bladder of *Noturus insignis* had a relative volume of only 4.6%. *Aphredoderus sayanus*, a bottom dwelling inhabitant of quiet water regions, also had a small swim bladder (3.6%). Pelagic, quiet water inhabitants, e.g., *Pomoxis nigromaculatus, Lepomis macrochirus,* and *Notemigonus crysoleucas* had large swim bladders (8.0-8.5%). Additionally, the factor analysis indicated relative volume of the swim bladder to covary with several other characters related with benthic habits (Factor 3, Fig. 3).

Comparisons of the actual magnitudes of the results listed above with a theoretical value which is assumed to give a fish neutral buoyancy are interesting. F.R.H. Jones (1951) calculated that if the average density of a fish were 1.076 g/cc, then a swim bladder volume equal to 7.06% of the total volume of the fish would be necessary to achieve hydrostatic equilibrium. Only a few species of fishes studied here showed mean values significantly different from this figure. *Notropis chiliticus, Noturus insignis, Umbra pygaea, Anguilla rostrata, Aphredoderus sayanus,* and all the darters had smaller percentage volumes and only *Pomoxis nigromaculatus* had a larger percentage volume than this theoretical figure. However, among the remaining species many significant differences did exist. These differences seem likely to reflect biological differences as stated above. Previously reported values of the percentage volume of the swim bladder in Cypriniformes have ranged from 5% to 10% (Alexander, 1959).

47. Relative length of the swim bladder was assumed to relate in the same way to the same qualities as relative volume of the same structure (Nelson, 1961; H.E. Evans, 1950). My results show that the ordination of species on this character would be similar to that obtained with the preceding (see listing above) and that the two characters are highly correlated (Pearson r = 0.88; $P < 0.001$). However, this character tends to have a stronger taxonomic component than the preceding. Thus even catfishes with fairly large relative swim bladder volumes (e.g., *Ictalurus punctatus*) have small relative swim bladder length. Suckers, especially those of the genus *Moxostoma* which have a three-part swim bladder, have large relative swim bladder lengths. Studies which encompass several families of teleosts and employ length of the swim bladder (or even length and depth but not width as Dobbin, 1941) as the sole estimator of buoyancy rest on shaky ground.

48. Relative gut length was assumed to be directly related to mud feeding, herbivory, and omnivory, and inversely related to carnivory and insectivory (H.E. Evans, 1950; Lagler et al., 1962; Forbes, 1888; Schmitz and Baker, 1969). My results support the "mud feeding" aspect especially, as positive correlations exist between this character and the presence of ostracods (P's < 0.02-0.002), diatoms (P's < 0.05-0.01), and silt ($P < 0.001$) in the gut.

49. Number of pyloric caeca was assumed to be correlated with the protein richness of the diet, as these structures function as an enzyme source and an area of absorption for protein nitrogen (Beamish, 1972; Phillips, 1969). My results show that the taxonomic component to this character was great. Thus, although some of the species for which I found piscivorous food habits (e.g., *Micropterus salmoides, Pomoxis nigromaculatus,* and *Centrarchus macropterus* – see Table 1) do have the most pyloric caeca, the most piscivorous of the fishes studied, *Esox niger*, lacks these structures.

50. Percentage of red muscle in the caudal peduncle was assumed to be directly proportional to the amount of sustained swimming or cruising that the fish does (Boddeke et al., 1959; Love, 1970; Gatz, 1973). Recently Roberts and Graham (1974) reported on the basis of electromyographic recordings that red muscle primarily is operating at slow swimming speeds in mackerel and that both red and white muscles increase in activity during acceleration.

The following listing of species by increasing percentage of red muscle corresponds generally to one's intuitive expectations given this function. Note sample size is 10 except for species in parentheses for which n = 1 or 2. Species mean percentages are: (*Umbra pygmaea* – 0%); *Etheostoma flabellare* – 0%; *E. fusiforme* – 0%; *E. olmstedi* – 0%; (*Percina crassa* – 0%); *Esox niger* – 1.8%; (*Enneacanthus gloriosus* – 2.2%); *Esox americanus* – 2.2%; *Aphredoderus sayanus* – 3.2%; *Pomoxis nigromaculatus* – 3.4%; *Lepomis cyanellus* – 3.9%; *Lepomis macrochirus* – 4.2%; *Lepomis gibbosus* – 4.2%; *Lepomis auritus* – 4.4%; *Micropterus salmoides* – 4.4%; *Gambusia affinis* – 4.5%; (*Anguilla rostrata* – 4.7%); *Erimyzon oblongus* – 4.7%; *Lepomis gulosus* – 4.7%; *Centrarchus macropterus* – 5.0%; (*Moxostoma anisurum* – 5.4%); *Perca flavescens* – 5.5%; *Notropis alborus* – 5.8%; *Phoxinus oreas* – 6.1%; *Ictalurus nebulosus* – 6.3%; (*Notropis hud-

sonius – 6.6%); (*Moxostoma erythrurum* – 6.7%); *Hybopsis hypsinotus* – 6.7%; *Notemigonus crysoleucas* – 6.7%; (*Ictalurus catus* – 7.5%); *Notropis procne* – 7.5%; *Catostomus commersoni* – 7.7%; (*Moxostoma pappillosum* – 8.4%); *Noturus insignis* – 8.5%; *Notropis altipinnis* – 8.8%; *Semotilus atromaculatus* – 9.2%; *Notropis cerasinus* – 9.2%; *Nocomis leptocephalus* – 9.7%; *Clinostomus funduloides* – 9.8%; *Notropis analostanus* – 9.9%; *Notropis ardens* – 11.1%; (*Moxostoma robustum* – 11.3%); *Notropis chiliticus* – 12.0%; and (*Ictalurus punctatus* – 14.2%).

Most of the work in the literature in which actual measurements of stamina for swimming in fishes were made has been for salmonids (e.g., Brett, 1965, 1967, 1973; Hammond and Hickman, 1966; Hochachka, 1961; Horak, 1969, 1972; D.R. Jones, 1971; Stevens, 1968; and Vincent, 1960); none of these fishes occur in my study streams. A few papers do report on such non-salmonids as goldfish (Fry, 1958), smallmouth bass (Larimore and Duever, 1968), largemouth bass (Laurence, 1972) and bluegills (Oseid and Smith, 1972). However, only the work by Houde (1969) and Bainbridge (1960) was of an interspecific comparative nature such that one could compare the swimming abilities for two or more species with red muscle content. Houde (op. cit.) found little difference between two species of percids with the 9 to 15 mm total length larvae that he used. Gatz (1973) speculated on the possible relationship between differences in swimming performance among the three species tested by Bainbridge (1960) and differences in red muscle content and concluded the relationship assumed in this paper seemed operative.

Supportive evidence of a somewhat different sort comes from the work of Reddy and Pandian (1974) on the predation effectiveness of *Gambusia affinis* in flowing water. In addition to giving data which indicate a halving of predatory efficiency, they reported that the *Gambusia* appeared to have lost much energy in the flowing water and appeared to have very little available to spare for predation. Such results correspond nicely with the low amount (4.5%) of red muscle I found in this species and the proposed interpretation of this character. A similar experiment would be interesting with a species such as *Notropis chiliticus* or *N. ardens*, both of which have more than twice the red muscle *Gambusia affinis* has.

A further point of interest about the percentage of red muscle in the peduncle concerns the probable selective forces involved in achieving the observed values for this character. An ability to cruise slowly for prolonged periods with low metabolic expenditure readily enough would "explain" selection for red muscle. But why do some species lack it entirely (e.g., *Etheostoma*) or have very little (e.g., *Esox* and *Umbra*)? Two points come to mind. First, some fishes move about slowly, seemingly entirely by the movement of the paired fins. *Esox* and *Umbra* are examples, and the fin musculature of these species is red muscle. Second, if red muscle were metabolically more costly to maintain than white in a resting state, then one would expect its presence to be selected against in those species which do not demonstrate slow cruising behavior. Some evidence of just such a higher metabolic rate for red muscle for white has been given by Gordon (1968) and Lin et al. (1974).

Brain characters

51. Relative size of the forebrain was assumed to be directly proportional to the importance of olfaction in the life of the fish (Tuge et al., 1968) and also with nocturnal habits (H.M. Evans, 1940).

52. Relative size of the optic lobes was assumed to be proportional to the importance of vision in the species (Schwassman and Kruger, 1968).

53. Relative size of the cerebellum was assumed to be large in active, quick swimming fishes and in forms which live in fast water, but small in sluggish, slow water fishes (Herrick, 1924; Schnitzlein,

1964; Miller and Evans, 1965).

54. Relative size of the vagal lobes was assumed to be positively correlated with "mouth tasting," i.e., eating mud which is then sorted to a degree in the mouth using taste buds of the mucous membrane of the posterior oral cavity (Bhimachar, 1935; H.E. Evans, 1952; H.M. Evans, 1940).

55. Relative size of the facial lobes was assumed to be directly proportional to the importance of lip and barbel tasting in the feeding behavior of the fish (H.M. Evans, 1940; H.E. Evans, 1952; Miller and Evans, 1965).

56. Relative size of the acoustic tubercles was assumed to be directly proportional to the importance of the lateral line system in the behavior of the fish (H.M. Evans, 1940; Tuge et al., 1968).

For all six characters relating to the hypertrophy of various lobes of the brain, my results placed at least some species for which behavior was known at seemingly appropriate positions in the ordinations obtained. For example, *Anguilla rostrata* and members of the genus *Ictalurus* have large forebrains; and cyprinids have relatively larger cerebellums than centrarchids. The assumption that other less known species were in appropriate relative positions did not seem unwarranted. Few studies have been done comparing the relative importance of different senses in feeding and thus, by assumption in this study, with the relative sizes of different brain lobes. The only such paper of which I am aware which involved a species in this study was that by Roberts and Winn (1962). They found *Etheostoma olmstedi* (I changed the nomenclature here to correspond with Cole, 1967, 1972) to rely much more heavily on sight than olfaction. This corresponds well with my results. I found that *E. olmstedi* had one of the smallest values for relative size of the forebrain and one of the largest for relative size of the optic lobes of all those species measured.

Caveats and Summation

Bock and von Wahlert (1965) point out that any particular anatomical feature or structure may serve multiple functions and thus be subject to natural selection as a part of any of several form-function complexes. They suggested that the biological role of any feature cannot be deduced from the mere study of the form-function complex, but must be determined by direct observation of the organism. Alternatively, it would seem that if natural selection has operated in a repeatable manner to cause a regular association between a particular morphological feature and one form-function complex, then evidence for this should exist as a constancy of utilized faculties for the particular feature. Specifically, there should be strong correlations between such a feature and some manifestation of its biological role and also there should be correlations between this feature and others associated with the same role. For example, if a principal selective pressure on mouth size is always prey size, then there should be a correlation between prey size and any measure of mouth size among a group of species of fishes and correlations between the various measures of mouth size.

The results presented above attest to the validity of both points of view. First, the many significant correlations indicate that some repeatable selective forces do seem to be governing some portion of the variation in the morphological features measured. This should not be surprising in that each character was chosen on the basis that I felt the strongest single selective force operating on it was recognizable and in that these selective forces were at times the same for more than one character. In a number of cases, e.g., relative width and height of the mouth, strong correlative evidence in support of the hypothesized adaptation has been given. On the other hand, only about 2% of the between character correlations have coefficients of determination greater than 50%. This dearth of high correlations, especially between characters assumed to be responding to similar selective forces, gives support to the viewpoint of Bock and von Wahlert (1965). That is, the variability seen between features of presumed close functional relation could well be the result of selective pressures for two (or more) different faculties operating on the same feature. Complex rather than simple causative patterns for the correlations observed seem likely.

All of the support for any particular ecological interpretation of morphological features provided by this study is of a correlative nature. As Sokal and Rohlf (1969, Fig. 15.5) so effectively illustrate, a large number of causal patterns can result in correlations and these patterns need to be sorted out. Certain types of information would greatly aid in this area. First, experimental studies analogous to those of Gee et al. (1974), Machniak and Gee (1975), and Werner (1974) are necessary for many more features. Second, direct observations of fishes in their natural habitats of the sort made by Keeleyside (1962) would be especially useful for many of the habitat related characters. Hopefully the present work will be of heuristic value in indicating some of the features about which observations might be made most gainfully.

In answer to the questions posed originally, this study indicates that some significant portion of the biology of a freshwater stream fish is determinable from its morphology. While it is well known that fishes exhibit extreme plasticity of behavior when raised in monospecies cultures, they do tend to specialize in the presence of other species and interspecific competition (Nilsson, 1955, 1960, 1963, 1965, 1967; Ivlev, 1961; Trojnar and Behnke, 1974; Griffith, 1974; Andrusak and Northcote, 1971). Gorman and Karr (1978) report that for stream fish communities these specializations occur primarily in the selection of specific habitat types and secondarily in the preference for certain food resources if several are readily available within a given habitat. Earlier literature (Thomas, 1962; Gibbons and Gee, 1972; Keast and Webb, 1966; Lindsey, 1963; Schutz and Northcote, 1972) and the present study both indicate that many of these specializations are related to morphology. The functions and biological roles that are regularly associated with many morphological features are given above.

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LITERATURE CITED

Aleev, Yu. G. 1969. Function and gross morphology in fish. Israel Program for Scientific Translations, Jerusalem (Transl. from Russian.) TT 67-51391.

Alexander, R. McN. 1959. The physical properties of the swimbladder in intact Cypriniformes. J. Exp. Biol. 36:315-332.

__________. 1967. Functional design in fishes. Hutchinson University Library, London.

Al-Hussaini, A.H. 1949. On the functional morphology of the alimentary tract of some fishes in relation to differences in their feeding habits. Anatomy and histology. Quart. J. Micr. Sci. 90: 109-139.

Andrusak, H., and T.G. Northcote. 1971. Segregation between adult cutthroat trout (*Salmo clarki*) and Dolly Varden (*Salvelinus malma*) in small coastal British Columbia lakes. J. Fish. Res. Bd. Canada 28:1259-1268.

Ashmole, N.P. 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). Syst. Zool. 17:292-304.

Bainbridge, R. 1960. Speed and stamina in three fish. J. Exp. Biol. 37:129-153.

Barlow, G.W. 1972. The attitude of fish eye-lines in relation to body shape and to stripes and bars. Copeia 1972:4-12.

Beamish, F.W.H. 1972. Ration size and digestion in largemouth bass, *Micropterus salmoides* Lacepede. Can. J. Zool. 50:153-164.

Bhimachar, B.S. 1935. A study on the correlation between the feeding habits and the structure of the hind brain in the South Indian cyprinoid fishes. Proc. Roy. Soc. Lond., B 117:258-272.

Bock, W.J., and G. von Wahlert. 1965. Adaptation and the form-function complex. Evolution 19: 269-299.

Boddoke, R., E.J. Slijper and A. van der Stelt. 1959. Histological characteristics of the body musculature of fishes in connèxion with their mode of life. Akademie van Wetenshappen Koninkl. Nederl. Proceedings C 62:576-588.

Branson, B.A., and G.A. Moore. 1962. The lateralis component of the acoustico-lateralis system in the sunfish family Centrarchidae. Copeia 1962:1-108.

Breder, C.M. Jr. 1926. The locomotion of fishes. Zoologica (New York) 4:159-297.

Brett, J.R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Bd. Canada 22:1491-1501.

__________. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. J. Fish. Res. Bd. Canada 24:1731-1741.

__________. 1973. Energy expenditure of sockeye salmon, *Oncorhynchus nerka*, during sustained performance. J. Fish. Res. Bd. Canada 30:1799-1809.

Bridge, T.W., and A.C. Haddon. 1889. Contributions to the anatomy of fishes. I. The airbladder and Weberian ossicles in the Siluridae. Proc. Roy. Soc. London 46:309-328.

Carpenter, K.E. 1940. The feeding of salmon parr in the Cheshire Dee. Proc. Zool. Soc. London 110:81-96.

Cole, C.F. 1967. A study of the eastern johnny darter, *Etheostoma olmstedi* Storer (Teleostei, Percidae). Ches. Sci. 8:28-51.

Cole, C.F. 1972. Status of the darters, *Etheostoma nigrum, E. longimanus* and *E. pondostomone* in Atlantic drainages (Teleostei, Percidae, subgenus *Boleosoma*), p. 119-138. *In*: The distributional history of the biota of the southern Appalachians. Part III: Vertebrates. P.C. Holt, R.A. Paterson, and J.P. Hubbard (eds.) Virginia Polytech Inst. and State Univ. Res. Div. Monograph 4, Blacksburg, Va.

Disler, N.N. 1971. Lateral line sense organs and their importance in fish behavior. Israel Program for Scientific Translations, Jerusalem. (Transl. from Russian.) TT 70-54021.

Dobbin, C.N. 1941. A comparative study of the gross anatomy of the air bladders of ten families of fishs of New York and other eastern states. J. Morphol. 68:1-29.

Evans, H.E. 1950. Structural modifications correlated with feeding habits in four species of cyprinid fishes. Unpubl. Ph.D. Dissertation, Cornell Univ., Ithaca.

__________. 1952. The correlation of brain pattern and feeding habits in four species of cyprinid fishes. J. Comp. Neur. 97:133-142.

Evans, H.M. 1940. Brian and body of fish. A study of brain pattern in relation to hunting and feeding in fish. The Blakiston Company, Philadelphia.

Forbes, S.A. 1880. The food of fishes. Bull. Ill. State Lab. Nat. Hist. 1(3):19-70.

__________. 1888. On the food relations of freshwater fishes: a summary and discussion. Bull. Ill. State Lab. Nat. Hist. 2(8):475-538.

__________, and R.E. Richardson. 1920. The fishes of Illinois. 2nd. ed. Natural History Survey of Illinois. Vol. III. Ichthyology. State of Illinois.

Fry, F.E.J. 1958. Approaches to the measurement of performance in fish, p. 93-97. *In*: The investigation of fish power problems. P.A. Larkin (ed.) H.R. MacMillan Lectures in Fisheries, Univ. of British Columbia.

Gatz, A.J. Jr. 1973. Speed, stamina, and muscles in fishes. J. Fish. Res. Bd. Canada 30:325-328.

__________. 1975. The ecology of fishes in three streams in North Carolina. Unpubl. Ph.D. Dissertation, Duke University, Durham.

__________. 1979. Community organization in fishes as indicated by morphological features. Ecology (in press).

Gee, J.H. 1968. Adjustment of buoyancy by longnose dace (*Rhinichthys cataractae*) in relation to velocity of water. J. Fish. Res. Bd. Canada 25: 1485-1496.

__________. 1970. Adjustment of buoyancy in blacknose dace, *Rhinichthys atratulus*. J. Fish. Res. Bd. Canada 27:1855-1859.

__________. 1972. Adaptive variation in swimbladder length and volume in dace, genus *Rhinichthys*. J. Fish. Res. Bd. Canada 29:119-127.

__________. 1974. Behavioral and developmental plasticity of buoyancy in the longnose, *Rhinichthys cataractae*, and blacknose, *R. atratulus*, (Cyprinidae) dace. J. Fish. Res. Bd. Canada 31: 35-41.

__________, K. Machniak and S.M. Chalanchuk. 1974. Adjustment of buoyancy and excess internal pressure of swimbladder gases in some North American freshwater fishes. J. Fish. Res. Bd. Canada 31:1139-1141.

Gibbons, J.R.H., and J.H. Gee. 1972. Ecological segregation between longnose and blacknose dace (genus *Rhinichthys*) in the Mink River, Manitoba. J. Fish. Res. Bd. Canada 29:1245-1252.

Gilbert, C.R. and R.M. Bailey. 1972. Systematics and zoogeography of the American cyprinid fish *Notropis (Opsopoeodus) emiliae*. Occ Pap. Mus. Zool., Univ. Michigan No. 664:1-35.

Gordon, M.S. 1968. Oxygen consumption of red and white muscles from tuna fishes. Science 159:87-90.

Gorman, O.T., and J.R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59: 507-515.

Gosline, W.A. 1971. Functional morphology and classification of teleostean fishs. Univ. Press of Hawaii, Honolulu.

__________. 1973. Considerations regarding the phylogeny of cypriniform fishes, with special reference to structures associated with feeding. Copeia 1973:761-776.

Gray, J. 1968. Animal locomotion. Weidenfeld and Nicolson, London.

Griffith, J.S. Jr. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in Idaho. Trans. Amer. Fish. Soc. 103:440-447.

Gromov, I.A. 1973. Morphological characteristics and local populations of the eastern carp [*Cyprinus carpio haematopterus* (Temm. et Schlegel)]. J. Ichthyology 13:335-347.

Hall, D.J., W.E. Cooper and E.E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15:839-928.

Hammond, B.R., and C.P. Hickman, Jr. 1966. The effect of physical conditioning on the metabolism of lactate, phosphate, and glucose in rainbow trout, *Salmo gairdneri*. J. Fish. Res. Bd. Canada 23:65-83.

Harman, H.H. 1967. Modern factor analysis. 2nd. ed. Univ. Chicago Press, Chicago.

Harris, J.E. 1937. The mechanical significance of the position and movements of the paired fins in the Teleostei. Pap. Tortugas Lab. 31:171-189.

__________. 1938. The role of fins in the equilibrium of the swimming fish: 2. The role of the pelvic fins. J. Exp. Biol. 15:32-47.

__________. 1953. Fin patterns and mode of life of fishes, p. 17-28. *In*: Essays in marine biology. S.M. Marshall and A.P. Orr (eds.) Oliver and Boyd, Edinburgh.

Herrick, C.J. 1924. Neurological foundations of animal behaviour. H. Holt and Company, New York.

Hespenheide, H.A. 1973. Ecological inferences from morphological data. Ann. Rev. Ecol. Syst. 4:213-229.

Himberg, K.-J.M. 1970. A systematic and zoogeographic study of some North European coregonids, p. 219-250. *In*: Biology of coregonid fishes. C.C. Lindsey and C.S. Woods (eds.) Univ. Manitoba Press, Winnipeg.

Hochachka, P.W. 1961. The effect of physical training on oxygen debt and glycogen reserves in trout. Can. J. Zool. 39:767-776.

Hora, S.L. 1922. Structural modifications in the fish of mountain torrents. Rec. Indian Mus., Calcutta 24:31-61.

__________. 1935. Ancient Hindu conception of correlation between form and locomotion of fishes. J. Asiatic Soc. Bengal. Science 1:1-7.

Horak, D.L. 1969. The effect of fin removal on stamina of hatchery-reared rainbow trout. Progr. Fish-Cult. 31:217-220.

__________. 1972. Survival of hatchery-reared rainbow trout (*Salmo gairdneri*) in relation to stamina tunnel ratings. J. Fish. Res. Bd. Canada 29: 1005-1009.

Houde, E.D. 1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). J. Fish. Res. Bd. Canada 26:1646-1659.

Hubbs, C.L. 1941. The relation of hydrological conditions to speciation in fishes, p. 182-195. *In*: A symposium on hydrobiology. Univ. of Wisconsin Press, Madison.

__________, and K.F. Lagler. 1958. Fishes of the Great Lakes region. Rev. ed. Cranbrook Institute of Science Bull. No. 26.

Hynes, H.B.N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven. (Transl. from the Russian by D. Scott.)

Jones, A.N. 1975. A preliminary study of fish segregation in salmon spawning streams. J. Fish. Biol. 7:95-104.

Jones, D.R. 1971. The effect of hypoxia and anaemia on the swimming performance of rainbow trout (*Salmo gairdneri*). J. Exp. Biol. 55:541-551.

Jones, F.R.H. 1951. The swimbladder and the vertical movements of teleostean fishes. 1. Physical factors. J. Exp. Biol. 28:553-566.

Kanep, S.V. 1971. Some aspects of the functional morphology of the lake pelyad [*Coregonus peled* (Gmelin)]. J. Ichthyology 11:855-866.

Keast, A. 1966. Trophic interrelationships in the fish fauna of a small stream. Proc. 8th Conf. Great Lakes Res. Div., Univ. Michigan Publ. 15:51-79.

__________, and D. Webb. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Bd. Canada 23:1845-1874.

Keenleyside, M.H.A. 1962. Skin-diving observations of Atlantic salmon and brook trout in the Miramichi River, New Brunswick. J. Fish. Res. Bd. Canada 19:624-634.

Kliewer, E.V. 1970. Gillraker variation and diet in lake whitefish *Coregonus clupeaformis* in northern Manitoba, p. 147-165. *In*: Biology of coregonid fishes. C.C. Lindsey and C.S. Woods (eds.) Univ. Manitoba Press, Winnipeg.

Kramer, E. 1960. Zur Form und Funktion des Lokomotionsapparates der Fische. Z. Wiss. Zool. 163:1-36.

Lagler, K.F. 1956. Freshwater fishery biology. 2nd. ed. Wm. C. Brown Company, Dubuque, Iowa.

__________, J.E. Bardach and R.R. Miller. 1962. Ichthyology. John Wiley and Sons, Inc., New York.

Larimore, R.W., and M.J. Duever. 1968. Effects of temperature acclimation on the swimming ability of smallmouth bass fry. Trans. Amer. Fish. Soc. 97:175-184.

Laurence, G.C. 1972. Comparative swimming abilities of fed and starved larval largemouth bass (*Micropterus salmoides*). J. Fish. Biol. 4:73-78.

Lin, Y., G.H. Dobbs, III and A.L. Devries. 1974. Oxygen consumption and lipid content in red and white muscles of Antarctic fishes. J. Exp. Zool. 189:379-385.

Lindsey, C.C. 1963. Sympatric occurrence of two species of humpback whitefish in Squanga Lake, Yukon Territory. J. Fish. Res. Bd. Canada 20: 749-767.

Lindstrom, T. 1955. On the relation fish size – food size. Fish. Bd. Sweden. Freshwater Res. Rep. No. 36:133-147.

Love, R.M. 1970. The chemical biology of fishes. Academic Press, New York.

Lundberg, J.G., and E. Marsh. 1976. Evolution and functional anatomy of the pectoral fin rays in cyprinoid fishes, with emphasis on the suckers (Family Catostomidae). Amer. Midl. Nat. 96: 332-349.

Machniak, K., and J.H. Gee. 1975. Adjustment of buoyancy by tadpole madtom, *Noturus gyrinus*, and black bullhead, *Ictalurus melas*, in response to a change in water velocity. J. Fish. Res. Bd. Canada 32:303-307.

Marshall, N.B. 1971. Explorations in the life of fishes. Harvard Univ. Press, Cambridge, Mass.

Martin, W.R. 1949. The mechanics of environmental control of body form in fishes. Publ. Ontario Fish. Res. Lab. No. 70.

Miller, R.J., and H.E. Evans. 1965. External morphology of the brain and lips of catostomid fishes. Copeia 1965:467-487.

Nelson, E.M. 1961. The comparative morphology of the definitive swim bladder in the Catostomidae. Amer. Midl. Nat. 65:101-110.

Nichols, J.T. 1915. On one or two common structural adaptations in fishes. Copeia 1915:19-21.

Nikolskii, G.V. 1933. On the influence of the rate of flow on the fish fauna of the rivers of central Asia. J. Anim. Ecol. 2:266-281.

_________. 1963. The ecology of fishes. Academic Press, New York. (Transl. from Russian by L. Birkett.)

Nilsson, N.-A. 1955. Studies on the feeding habits of trout and char in north Swedish lakes. Fish. Bd. Sweden. Freshwater Res. Rep. Drottningholm No. 36:163-225.

Nilsson, N.-A. 1958. On the food competition between two species of *Coregonus* in a north-Swedish lake. Fish. Bd. Sweden. Freshwater Res. Rep. Drottningholm No. 39:146-161.

_________. 1960. Seasonal fluctuations in the food segregation of trout, char and whitefish in fourteen north-Swedish lakes. Fish. Bd. Sweden. Freshwater Res. Rep. Drottningholm No. 41: 185-205.

_________. 1963. Interaction between trout and char in Scandinavia. Trans. Amer. Fish. Soc. 92:276-285.

_________. 1965. Food segregation between salmonid species in north Sweden. Fish. Bd. Sweden. Freshwater Res. Rep. Drottningholm No. 46:58-78.

_________. 1967. Interactive segregation between fish species, p. 295-313. *In*: The biological basis of freshwater fish production. S.D. Gerking (ed.) John Wiley and Sons, Inc., New York.

Northcote, T.G. 1954. Observations on the comparative ecology of two species of fish, *Cottus asper* and *Cottus rhotheus*, in British Columbia. Copeia 1954:25-28.

Nursall, J.R. 1958. The caudal fin as a hydrofoil. Evolution 12:116-120.

Oseid, D., and L.L. Smith, Jr. 1972. Swimming endurance and resistance to copper and malathion of bluegills treated by long-term exposure to sublethal levels of hydrogen sulfide. Trans. Amer. Fish. Soc. 101:620-625.

Ovchinnikov, V.V. 1971. Swordfishes and billfishes in the Atlantic Ocean. Ecology and functional morphology. Israel Program for Scientific Translations, Jerusalem. (Transl. from Russian.) TT 71-50011.

Pianka, E.R. 1969. Sympatry of desert lizards (*Ctenotus*) in western Australia. Ecology 50:1012-1030.

Phillips, A.M. Jr. 1969. Nutrition, digestion, and energy utilization, p. 391-432. *In*: Fish physiology. Vol. I. W.S. Hoar and D.J. Randall (eds.) Academic Press, New York.

Protasov, V.R. 1970. Vision and near orientation of fish. Israel Program for Scientific Translations, Jerusalem. (Transl. from Russian.) TT 70-50065.

Reddy, S.R., and T.J. Pandian. 1974. Effect of running water on the predatory efficiency of the larvivorous fish *Gambusia affinis*. Oecologia (Berl.) 16:253-256.

Roberts, J.L., and J.B. Graham. 1974. Swimming and body temperature of mackerel. Amer. Zool. 14:1258 (Abstr.)

Roberts, N.J., and H.E. Winn. 1962. Utilization of the senses in feeding behavior of the johnny darter, *Etheostoma nigrum*. Copeia 1962:567-570.

Schmitz, E.H., and C.D. Baker. 1969. Digestive anatomy of the gizzard shad, *Dorosoma cepedianum* and the threadfin shad, *D. petenense*. Trans. Amer. Microsc. Soc. 88:525-546.

Schnitzlein, H.N. 1964. Correlation of habitat and structure in the fish brain. Amer. Zool. 4:21-32.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704-726.

_________, and G.C. Gorman. 1968. Some niche differences among three species of Lesser Antillean anoles. Ecology 49:819-830.

Schutz, D.C., and T.G. Northcote. 1972. An experimental study of feeding behavior and interaction of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). J. Fish. Res. Bd. Canada 29:555-565.

Schwartz, F.J., and B.W. Dutcher. 1962. Tooth replacement and food of the cyprinid, *Notropis cerasinus*, from the Roanoke River, Virginia. Amer. Midl. Nat. 68:369-375.

Schwassmann, H.O., and L. Kruger. 1968. Anatomy of visual centers in teleosts, p. 3-16. *In*: The central nervous system and fish behavior. E. Ingle (ed.) Univ. Chicago Press, Chicago.

Sokal, R.R., and F.J. Rohlf. 1969. Biometry. W.H. Freeman and Company, San Francisco.

Starck, W.A. II, and R.E. Schroeder. 1970. Investigations on the gray snapper, *Lutjanus griseus*. Stud. Trop. Oceanogr. Miami 10.

Stevens, E.D. 1968. The effect of exercise on the distribution of blood to various organs in rainbow

trout. Comp. Biochem. Physiol. 25:615-625.
Swynnerton, G.H., and E.B. Worthington. 1940. Note on the food of fish in Haweswater (Westmorland). J. Anim. Ecol. 9:183-187.
Thomas, J.D. 1962. The food and growth of brown trout (*Salmo trutta* L.) and its feeding relationships with the salmon parr (*Salmo salar* L.) and the eel [*Anguilla anguilla* (L.)] in the River Teifi, West Wales. J. Anim. Ecol. 31:175-205.
Trojnar, J.R., and R.J. Behnke. 1974. Management implications of ecological segregation between two introduced populations of cutthroat trout in a small Colorado lake. Trans. Amer. Fish. Soc. 103:423-430.
Tuge, H K. Uchihashi and H. Shimaura. 1968. An atlas of the brains of fishes of Japan. Tsukiji Shokan Publ. Co., Tokyo.
Vincent, R.E. 1960. Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchill). Trans. Amer. Fish. Soc. 89: 35-52.
Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Bd. Canada 31:1531-1536.

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NICHE RELATIONSHIPS OF *THAMNOPHIS RADIX HAYDENI* AND *THAMNOPHIS SIRTALIS PARIETALIS* IN THE INTERLAKE DISTRICT OF MANITOBA

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ABSTRACT

The niches occupied by the western plains garter snake (*Thamnophis radix haydeni*) and the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake district of Manitoba were compared with respect to feeding habits and six environmental factors. The species were studied both in allopatry and in sympatry.

Thamnophis sirtalis occurring in sympatry with *T. radix* altered its feeding habits, but not in such a way as to produce niche displacement. Its feeding habits did not differ significantly from those of *T. radix* either in allopatry or in sympatry. Changes in its feeding habits are attributed to changed in the relative availability of food items.

Of the environmental factors examined, habitat, air temperature and substrate temperature contributed most strongly to niche discrimination in allopatry. *Thamnophis radix* occurred near meadow ponds at high air but low substrate temperatures and *T. sirtalis* occurred near fen-like marshes of the aspen forest at lower air but higher substrate temperatures. In sympatry the contributions of habitat and air temperature to niche discrimination were reduced, whereas those of light intensity and substrate temperature were increased, *T. radix* selecting a higher value of both than *T. sirtalis*. This shift in the importance of environmental factors to niche discrimination need not be attributed to species interaction but may be explained in terms of behavioral compensation for concurrent changes in the available niche. The shift was partially produced by changes in the daily activity pattern, towards midday for *T. radix* and towards morning and evening for *T. sirtalis*.

INTRODUCTION

The summer niche requirements of garter snakes are poorly known and the degree of competitive interaction between species is not known at all. Food and habitat utilization (Carpenter, 1952; Fleharty, 1967) and food utilization (Fouquette, 1954) have been compared for sympatric populations of garter snakes species in three widely separated localities. None of these authors, however, obtained detailed comparative data for allopatric populations of the same species. Niche displacement among sympatric garter snakes, while suggested by these authors as a possible explanation for resource partitioning, has seldom been properly examined. A notable exception is the work of White and Kolb (1974) on sympatric populations of two garter snake species in California, one of which is represented by a nearby allopatric population.

In the Interlake district of Manitoba two garter snake species occur: the western plains garter snake (*Thamnophis radix haydeni* Kennicott) and the red-sided garter snake (*Thamnophis sirtalis parietalis* Say). While the range of overlap between these species is limited, both occur in sufficiently large numbers to allow the collection of adequate samples from within this range. The present study compares the niches occupied by these two species, both within the range of overlap and beyond it, to determine whether any changes in the relative niche positions were occurring that could be attributed to the presence or absence of a congeneric species rather than to changes in the available niche.

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MATERIALS AND METHODS

Field Study.—The study area is located approximately between 50° N and 51° N latitude and between 97° W and 98° W longitude. It is bounded on the east by Lake Winnipeg and on the west by Lake Manitoba as outlined in Figure 1. Snakes were captured within this area from May through August of 1973 and from June through August of 1974. The sampling effort in 1974 was concentrated within a region defined on the basis of the first summer's sampling and included all quarter-townships (23.4 km^2) in which both *T. radix* and *T. sirtalis* had been captured. This region of sympatry is shown in Figure 1. Severe flooding in May of 1974 prevented sampling before June.

Snakes were found by searching on foot in the vicinity of water and were captured by hand. Preliminary sampling had shown that garter snakes in the Interlake district were seldom found far from a water body of some sort. Snakes seen crossing roads were not captured since the road habitat is not a natural one and cannot be avoided by snakes in their movements. The sampling effort was spread over the daylight hours from sunrise to sunset since preliminary attempts to find snakes at night had proven unproductive. No systematic sampling plan was followed due to the difficulty of collecting large samples without being somewhat opportunistic in allocation of the sampling effort. Any developing bias in collection with respect to time of day, geography or weather condi-

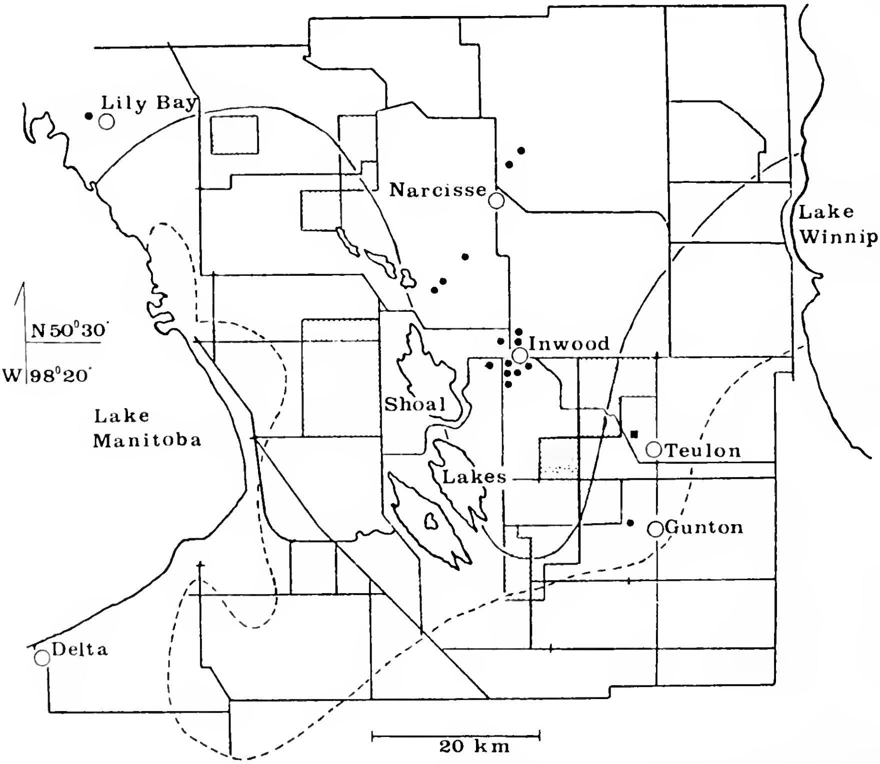

Fig. 1. Map of the study area showing major roads, towns (open circles) and approximate lines of continuous (solid) and discontinuous (dashed) aspen forest. Areas included in the sympatric region are stippled. All other areas are included in the allopatric region. The known communal den of *T. radix* (solid square) and known communal dens of *T. sirtalis* (solid circles) are located.

tions was soon detected from field records and appropriate corrections were made.

The feeding habits of *T. radix* and *T. sirtalis* were examined by palpating the stomachs of all snakes captured to force regurgitation of recently eaten food. Due to the difficulty of determining the number of prey represented in partially digested remains, only the presence, and not the number, of food items of each type found in a snake was recorded.

Six environmental factors were recorded at all capture sites to determine the relative importance of each of these factors as niche dimensions. A niche dimension is defined here as any factor serving to separate species ecologically (Levins, 1968) and the importance of an environmental factor refers here to its value in separating *T. radix* and *T. sirtalis* ecologically. Since biotic, physical and temporal environmental factors were considered, the term "environmental factors" is used in its broadest sense. However, the environmental factors considered were all judged capable, a priori, of eliciting direct response from a snake.

Habitat was classified as an environmental factor according to the type of water body nearest the capture site of a snake. Water was usually available within several hundred meters of a capture site. Three habitat classes that reflected the proportion of water surface area covered by a sedge mat were recognized. A sedge mat was composed of moss and old sedge decaying just beneath the surface of the water and was overlain by the previous year's growth of sedge, which was folded to form a compact horizontal network at or above the surface of the water. Habitat classes included ponds (no sedge mat; sharp interface between land and water), open marshes (sedge mat at the edges only; open water or sparse emergent vegetation dominant) and closed marshes (dominated by sedge mat; little or no open water). The terminology of aquatic communities in the aspen forest and parkland has not been standardized. Ponds in the study area conformed to the definition of Radforth (1964). Cover was readily available only in the form of shrubbery or small mammal burrows. Large rocks and logs were rare and did not seem to be used for cover. Heinselman (1963) included the marsh types referred to here as open and closed in his definition of marsh. Closed marshes in the study area resembled fens but were neither sufficiently peaty nor sufficiently patterned to conform well to Heinselman's definition of that term. Cover was readily available in the form of sedge mat and encroaching aspen forest. Habitat classes were coded in the above order from 1 through 3. They were judged to be sufficiently discrete in nature to warrant the use of a discrete variable as a numerical code. A transition from the first habitat class to the last was apparent on a south-west to north-east cline through the study area and corresponded to a transition from parkland to aspen forest.

Substrate moisture was classified as an environmental factor on the basis of a simple test performed at the capture site of a snake. If water could not be forced through the fingers by pressing the back of the hand against the substrate with as much force as possible, the substrate was termed dry. If water could just be forced through the fingers by similar action, the substrate was termed damp. If the cup of the hand could be filled with water by similar action, the substrate was termed waterlogged. Two additional moisture classes included standing water (with emergent vegetation) and open water (with no emergent vegetation). Moisture classes were coded in the above order from 1 through 5. This crude method of quantifying substrate moisture seemed to correlate well with the amount of water at the surface although it was certainly not a perfect linear measure. It was considered preferable to measurements of water content from soil samples since the latter reflected moisture beneath the surface, which often differed markedly from that found at the surface.

Light intensity incident upon the snake at the precise point where it was originally seen was measured as an environmental factor with a Vivitar photographic light meter (Model 43). The meter was sensitive only to visible light. Intensity was recorded in units of exposure value (EV) at an ASA setting of 100 with the light meter pointed directly at the sun.

Air temperature at substrate level was recorded at all capture sites with Yellow Springs Incorporated (YSI) thermistors (Models 43TD and 42SC) and YSI probes (Model 402). The probe was held in the body shadow of the investigator as close to the substrate surface as possible without contact.

Substrate temperature was recorded at all capture sites with the same thermistors. Since substrate temperature near the surface was extremely sensitive to the depth and exact location of the thermistor probe, temperatures were taken at a depth of 5 cm below the surface. Although this procedure minimized measurement error due to minor variations in probe position it must be noted that temperatures at this depth often differ from those experienced by a snake at the contact surface. When snakes were found upon a vegetation mat the surface was defined at the level of the highest part of the snake's body that was in contact with the vegetation.

Time of capture of each snake was recorded as an environmental factor on the daylight-saving time scale. It was coded as an absolute deviation (in hours) from 1400 hours (2 P.M. and the approximate midpoint of the day) so as to reflect the degree of mid-day activity of the snakes. No distinction was made with this time scale between morning and evening, so that the scale would correlate roughly with diel variations in environmental temperature and light intensity. Such a scale was desirable in order that the degree of correlation of time of capture with temperature or light intensity at capture sites would serve as an indicator of the extent to which snakes were making use of diel variations in selecting environmental temperatures or light intensities.

The six environmental factors described above were felt to be of potential importance in characterizing and distinguishing between the niches of *T. radix* and *T. sirtalis*. For an environmental factor to be important in this sense it is necessary, though not sufficient, that the snakes be sensitive to it. One way in which all of the environmental factors measured seemed potentially capable of affecting a snake was by means of influencing its body temperature. To detect such influences both oral and cloacal body temperatures of the snakes were taken along with measurements of the six environmental factors at each capture site. The same thermistors used to record air and substrate temperatures were used for this purpose. Body temperatures were always taken immediately upon capture and with minimal handling of the animals. The two body temperatures were taken consecutively and in no particular order.

Data of the type described above were taken from snakes captured in allopatric and sympatric regions in the summer of 1973. An additional sample of snakes was collected from within the sympatric region in the summer of 1974. Data from this sample were pooled with those taken from the same region the year before.

Analytical Methods.—Feeding habits of *T. radix* and *T. sirtalis* were compared, both in allopatric and in sympatric regions, using a 2xC contingency chi-square test for association between species and food type utilized. Feeding habits in allopatric and sympatric regions were also compared, both for *T. radix* and *T. sirtalis*, using a 2xC contingency chi-square test for association between region and food type utilized. Columns were pooled in all contingency tables to produce expected values greater than 1.

Sampling effort in the field was estimated for each species in hours spent searching for snakes within its range. Daily profiles of catch per unit effort, calculated for hourly intervals throughout the course of the day, were compared between *T. radix* and *T. sirtalis* both in allopatric and in sympatric regions. For intervals in which less than three search hours had been spent catch per unit effort was not calculated.

Slight biases often developed in the sampling effort before they were noticed and corrected. The effort spent searching for *T. radix* and *T. sirtalis* varied slightly throughout the summer in favor of either one species or the other. Since the range of environmental factors available to the snakes also varied throughout the course of the summer, such disparate seasonal allocation of the sampling effort was likely to produce spurious differences between species in the range of environmental factors measured at capture sites. Therefore, seasonal trends in environmental factors were quantified so that environmental data from capture sites could be adjusted for these trends by covariance, using powers of the date (day of the year and day^2) as covariates. This method of compensating for seasonal effects in long term data was used by Green (1974) in a similar type of study. It allowed description of seasonal trends in the environmental factors as parabolic curves. On the basis of visual inspection of the scatter of points about these curves, this description was considered to be adequate.

The frequency distributions of environmental factors were often non-normal. Medians often differed significantly from the means indicating skewness, and 95% confidence intervals on individual observations often exceeded or fell short of the measured range indicating kurtosis. With large samples non-normality has little effect upon comparisons of the means either by univariate (Scheffe, 1959) or by multivariate (Ito *in* Krishnaiah, 1969) methods, although it may influence comparisons of variance and covariance more strongly. Heterogeneity of variance, which often accompanies non-normality, was considered more of a problem. Press (1972) cautions that although univariate comparisons of means are little affected by heterogeneity of variance when sample sizes are large, most assertions about robustness with respect to the assumption of homogeneity of variance in the multivariate case are speculative. The reliability of multivariate methods must therefore be considered uncertain to the extent that this assumption is violated. Adjustment of environmental data for seasonal trends, as described above, improved multivariate homogeneity of variance and covariance in the present study.

The means of environmental factors for *T. radix* and *T. sirtalis* were compared both by univariate and multivariate methods. Large sample normal deviate tests were used for univariate comparisons. These were applied to environmental data that had not been adjusted for seasonal trends since the seasonal trends shown by two of the environmental factors differed significantly between species. In these cases the description and use of common seasonal trends to adjust the environmental data for long term effects was not strictly justified. Discriminant function analysis (Cooley and Lohnes, 1971) was used for multivariate comparison of environmental factors between *T. radix* and *T. sirtalis*. Environmental data for use in discriminant function analysis were adjusted for seasonal trends since this procedure improved multivariate homogeneity of variance and covariance. The use of seasonally adjusted data may have been somewhat artificial since not all environmental factors showed seasonal trends that were common to both species. However, uncertainty about the robustness of multivariate methods to violations of the homogeneity of variance assumption made the use of seasonally adjusted environmental data preferable for multivariate comparison. Multivariate comparison was considered more informative than univariate comparison because it takes correlations between the environmental factors into consideration.

The method of discriminant analysis as used here is analogous to a multiple regression of a dependent variable reflecting species membership upon a set of environmental factors. Environmental factors which contribute strongly to discrimination between the niches of *T. radix* and *T. sirtalis* are weighted heavily in the multiple regression equation, or discriminant function, so as to maximize the ratio of between species to within species variability in the predicted values of the dependent species variable. These predicted values are called discriminant scores. Each snake was therefore assigned a discriminant score which was a linear function of the environmental factors measured at its capture site. The difference between the mean discriminant score of *T. radix* and *T. sirtalis* is a measure of the overall ecological distance between their niches. An increase in this distance when snakes are collected from a region of sympatry can be taken as evidence of niche displacement.

The magnitude of the weight assigned to an environmental factor in the discriminant function depends not only upon the importance of that factor to species discrimination but also upon the magnitude of its measurement units. Standardization of all weights equalizes the scale of measurement so that the standardized weights represent the relative proportion of species discrimination contributed to the function by each environmental factor. Multiplication of these standardized weights by the discriminating power of the entire function gives an index of the ecological importance of each factor which can be compared between different discriminant functions. The measure of discriminating power used here was the squared canonical correlation coefficeint between the species variable and the environmental factors. This measure represents the fraction of variation in species membership explained by the discriminant function. The index so produced was used to compare the ecological importance of environmental factors between allopatric and sympatric regions. The sign of this index for any one factor indicated the relative position of *T. radix* and *T. sirtalis* on that environmental gradient. A negative sign indicated that *T. radix* was found at the lower end of that gradient and *T. sirtalis* at the upper end.

To determine the degree of dependence of body temperatures upon the environmental factors, multiple regressions of oral and cloacal temperatures on these factors were calculated separately for *T. radix* and *T. sirtalis*. Normal deviate tests were used to compare slopes and intercepts between species.

RESULTS

In the summer of 1973, 137 *T. radix* and 128 *T. sirtalis* were captured. Of these 32 *T. radix* and 36 *T. sirtalis* were found within the sympatric region. An additional sample of 73 *T. radix* and 32 *T. sirtalis* was collected from within the sympatric region in the summer of 1974.

Feeding Habits.—From Table 1 it was apparent that there were no differences in the feeding habits of *T. radix* and *T. sirtalis* either in the allopatric region ($X_7^2 = 9.66$; $P > .01$) or in the sympatric region ($X_6^2 = 10.47$; $P > .01$). The feeding habits of *T. radix* did not differ between allopatric and sympatric regions ($X_8^2 = 11.68$; $P > .01$). The feeding habits of *T. sirtalis* did differ between allopatric and sympatric regions ($X_4^2 = 13.42$; P .01). The change involved an increased utilization in the sympatric region of wood frogs (*Rana sylvatica*) and a decreased utilization of chorus frogs (*Pseudacris triseriata*).

Environmental Factors. — Seasonal trends in the environmental factors were adequately described as parabolic functions of the date. Habitat, as recorded at capture sites, was affected by seasonal movements of the snakes in the allopatric region. As *T. sirtalis* moved north in the fall towards its denning sites (Gregory and Stewart, 1975) it was found more frequently near the closed marshes of the aspen forest. A slight shift in *T. radix* towards the ponds of the open parkland to the south was not significant, but the trends for *T. radix* and *T. sirtalis* differed significantly from one another in the allopatric region. In the restricted sympatric region seasonal movements of the snakes had less effect on habitat classes and no significant seasonal trends were shown. Moisture, as recorded at capture sites, decreased throughout the summer in the allopatric region as water bodies dried up. In the sympatric region, flooding in the spring of 1974 increased July moisture levels at capture sites. This effect was not apparent until July because the flooding restricted snake collection in June. The effect was more pronounced for *T. radix* than *T. sirtalis* because the proportion of *T. sirtalis* taken in the sympatric region during the summer of 1974 was severely reduced due to drowning at dens in the spring. This produced significant differences between *T. radix* and *T. sirtalis* in the seasonal trends shown by moisture within the sympatric region, even though their individual trends were not significant. Light intensity decreased throughout the summer as the azimuth of the sun decreased. Air and substrate temperatures peaked in mid-summer. Time of capture of the snakes, expressed as a deviation from mid-day, showed no significant seasonal trends.

Univariate comparisons of environmental factor means between the niches of *T. radix* and *T. sirtalis*, applied to environmental data that had not been adjusted for seasonal trends, showed interspecific differences in habitat, moisture, air temperature and substrate temperature to be significant ($P < .01$) in the allopatric region (Fig. 2). Similar comparisons in the sympatric region showed significant ($P < .01$) interspecific differences in habitat, light intensity and substrate temperature.

These differences remained apparent after adjustment of the environmental data for seasonal trends. Discriminant scores derived from seasonally adjusted environmental data gave better discrimination between the niches of *T. radix* and *T. sirtalis* than did any single environmental factor, both in allopatric and in sympatric regions, but did not give any evidence of niche displacement. On the contrary, discriminant scores became more similar in the sympatric region than in the allopatric region (Fig. 3). Multivariate results agreed well with those derived by univariate methods, although some differences were apparent (Table 2). The index of ecological importance, derived from the weights in the discriminant function, was large for habitat, both in allopatric and in sympatric regions, although it became smaller in the sympatric region, indicating reduced importance there. The negative sign of this index indicates that *T. radix* occupied the lower end of the habitat gradient (ponds) and *T. sirtalis* the upper end (closed marshes). Substrate moisture, in contast to univariate results, was not ecologically important in either region. Light intensity was important only in the sympatric region with *T. radix* occupying the upper (sunny) end of the gradient whereas air temperature was important only in the allopatric region, with *T. radix* occupying the upper (warm) end of the gradient. Substrate temperature was important in both allopatric and sympatric regions, although it become more important in the latter region. Associated with the increased importance of this factor in the sympatric region, in contrast to univariate results, was a reversal in the relative species positions on the gradient, *T. radix* coming to occupy the upper (warm) rather than the lower (cool) end. Time of capture, expressed as a deviation from mid-day, was not an ecologically important factor in either the allopatric or the sympatric region. These results agree with those based on univariate comparisons, although in the sympatric region they give considerably less importance to the time factor.

Thermal Relations.—Oral and cloacal temperatures of *T. radix* were significantly higher ($P < .01$) than those of *T. sirtalis* in the allopatric region only. Body temperatures of *T. sirtalis* increased significantly (oral $P < .05$; cloacal $P < .01$) in the sympatric region (Fig. 4). Frequency distributions of body temperatures were negatively skewed, as shown by the fact that the median temperatures were always higher than the means, indicating that occasionally exceptionally cold snakes were encountered.

Multiple regression showed oral temperatures of *T. radix* to depend most strongly upon light intensity, air temperature and substrate temperature (Table 3). Cloacal temperatures of *T. radix* depended most strongly upon the same three environmental factors. Of these three factors air temperature was most important. Oral temperatures of *T. sirtalis* also depended most strongly upon light intensity, air temperature and substrate temperature. Habitat exerted an additional effect upon oral temperatures of *T. sirtalis*, over and above that produced by the other environmental factors, oral temperatures being lower in the closed marsh. Cloacal temperatures of *T. sirtalis* depended most strongly upon air temperature and substrate temperature and were independent of light intensity. Cloacal temperatures, like oral temperatures, were lower in the closed marsh, other environmental factors being equal. An additional effect seemed to be exerted upon the cloacal temperatures of *T. sirtalis* by substrate moisture and time of capture, cloacal temperatures being higher at moist capture sites and lower near mid-day, other factors being equal. The relationships of oral and cloacal temperature to the habitat factor differed significantly ($P < .01$) between *T. radix* and *T. sirtalis*, being negative for *T. sirtalis* only. The relationships of cloacal temperature to substrate moisture, substrate temperature and time of capture differed significantly ($P < .01$) between *T. radix* and *T. sirtalis*, being more positive for *T. sirtalis*.

Activity.—A bimodal pattern of daily activity was suggested by daily profiles of catch per search hour in the field for both *T. radix* and *T. sirtalis* in the allopatric region (Fig. 5). Effort in this region ranged from 3 to 22 search hours per hourly time interval. In the sympatric region the morning and evening peaks of activity for *T. sirtalis* were farther apart than in the allopatric region, while *T. radix* eliminated its morning peak and became more active towards mid-day. Effort in this region ranged from 4 to 41 search hours per hourly interval and catches were generally lower for both species than in the allopatric region.

DISCUSSION

Feeding Habits.—Both *T. radix* and *T. sirtalis* appeared to feed opportunistically, taking a wide variety of food items in rough proportion to their apparent abundance. This may be considered an adapta-

TABLE 1. Number of *T. radix* and *T. sirtalis* stomachs containing various food items in allopatric and sympatric regions.

FOOD CLASS	Allopatric Region *T. radix*	 *T. sirtalis*	Sympatric Region *T. radix*	 *T. sirtalis*
Rana sylvatica	24	15	36	24
Rana pipiens	4	0	3	0
Pseudacris triseriata	8	11	7	4
Hyla versicolor	2	2	1	3
Bufo	3	3	4	2
Tadpoles	5	0	1	0
Rodentia	1	0	1	0
Oligochaeta	5	2	0	0
Hirudinea	6	6	6	0
Gastropoda	0	0	2	0

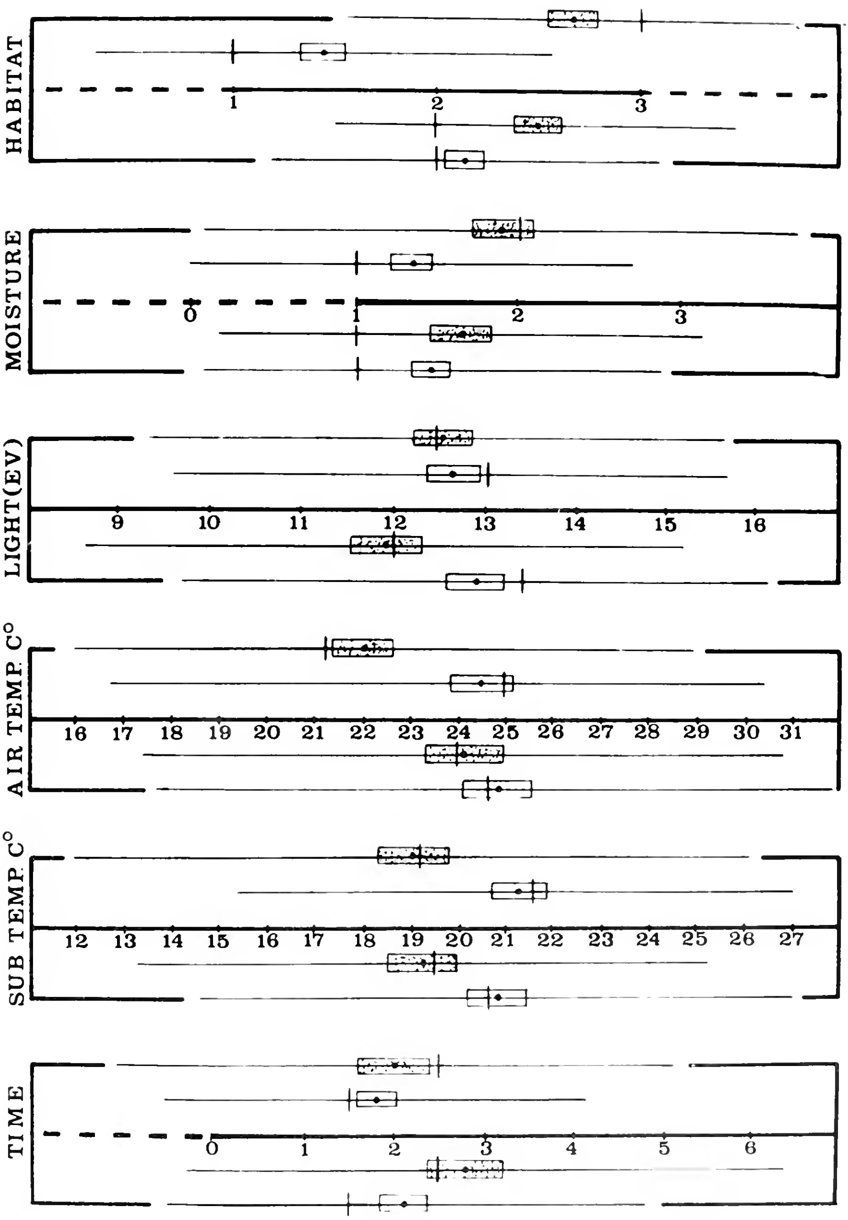

Fig. 2. Location of *T. radix* (open rectangles) and *T. sirtalis* (stippled rectangles) on gradients of the six environmental factors measured at capture sites. Rectangles indicate 95% confidence intervals on the means (solid circles). Medians (vertical lines) and 95% confidence intervals on the observations (horizontal lines) are also shown. The axis of an environmental factor is broken beyond the measured range of that factor. Statistics above the axis pertain to the allopatric region. Statistics below the axis pertain to the sympatric region.

Time is measured in units of hours + 2 P.M. Habitat code 1 = pond; 2 = open marsh; 3 = closed marsh. Moisture code 1 = dry; 2 = damp; 3 = waterlogged; 4 = standing water; 5 = open water.

tion to the short growing season encountered in the temperate zone. In contrast to the studies of Carpenter (1952), Fouquette (1954) and Fleharty (1967), who worked with different species combinations, no differences were found between the feeding habits of *T. radix* and *T. sirtalis* in sympatry. Gregory's (1977a) limited observations on the feeding habits of *T. radix* captured largely in sympatry with *T. sirtalis* invited similar conclusions. Although *T. sirtalis* altered its feeding habits in the sympatric region, it did not do so in such a way as to displace its niche from that of *T. radix*. The major changes involved an increased utilization of wood frogs and a decreased utilization of chorus frogs. These changes may have been the result of variations in the relative availability of wood frogs and chorus frogs. Since there was no niche displacement in sympatry with respect to feeding habits, the changes cannot be attributed to species interaction. White and Kolb (1974), in their study of two garter snakes species in California, similarly rejected the hypothesis of competitive displacement since changes in the feeding habits of *T. sirtalis fitchi*, when in sympatry with *T. elegans*, were not in the direction of niche displacement. They felt that feeding habits were determined largely by availability, which interpretation is also suggested in the present study.

Enviornmental Factors.—In the allopatric region, habitat, air temperature and substrate temperature contributed most strongly to niche discrimination (Table 2). *Thamnophis radix* occurred near ponds at high air but low substrate temperatures while *T. sirtalis* occurred near marshes at lower air but higher substrate temperatures. Although univariate comparisons between *T. radix* and *T. sirtalis* also attributed importance to substrate moisture, multivariate results indicated that this factor was superfluous due to its strong correlation with other environmental factors of greater value in discriminating between species. Substrate temperature was a particularly strong negative correlate of substrate moisture.

The ecological importance of habitat can be related to the thermal responses of the snakes. Habitat exerted an independent effect upon both oral and cloacal temperatures of *T. sirtalis*; this was probably due to the shade provided by the sedge mat in the closed marsh. Large expanses of sedge mat with associated stands of aspen forest provide a readily accessible thermal refuge. This type of cover may have been particularly important to *T. sirtalis*, which is more darkly colored than *T.*

TABLE 2. Discriminant function coefficients (unstandardized) and indices of discriminating value derived from them in allopatric and sympatric regions.

ALLOPATRIC	Habitat	Moisture	Light	Air Temp.	Sub. Temp.	Time	R_c^2*
Coefficient	-30.729	-2.922	2.021	1.110	-1.227	-1.703	.54
Index**	- .502	- .066	.085	.117	- .103	- .069	

SYMPATRIC	Habitat	Moisture	Light	Air Temp.	Sub. Temp.	Time	R_c^2*
Coefficient	-6.117	-0.243	1.660	-0.105	0.577	-0.661	.25
Index**	- .163	- .010	.142	- .022	.104	- .055	

*R_c^2 = Squared cannonical correlation coefficient (fraction of variation in species membership accounted for by the discriminant function)

**Standardized discriminant function coefficients multiplied by R_c^2.

radix in the Interlake district and perhaps subject to overheating in the summer (Hart, 1975). Such cover was conspicuously absent from the pond habitat utilized extensively by *T. radix*. Cover was similarly important to niche discrimination in the studies of Carpenter (1952) and Fleharty (1967).

The importance of air and substrate temperature to niche discrimination in the allopatric region also reflects the thermal relations of the snakes. Both factors exerted a strong effect upon oral and cloacal temperatures of *T. radix* and *T. sirtalis*. Since *T. radix* is lighter in color than *T. sirtalis* in the Interlake district, it may have been better adapted to the higher air temperatures that characterized its range and able to tolerate them by seeking out low substrate temperatures. *Thamnophis sirtalis* was apparently unable to tolerate high air temperatures without a thermal refuge in the form of closed marsh or aspen forest and, probably for this reason, it did not occur much beyond the range of these habitat types. Fleharty (1967) similarly found air and substrate temperatures to be useful in defining the niches of garter snake species.

In the restricted sympatric region, the available range of environmental factors was probably reduced. As a result, the importance of habitat and air temperature to niche discrimination was also reduced, the latter becoming insignificant. However, the importance of substrate temperature and light intensity at capture sites was increased (Table 2). This can only be interpreted as a behavioral reaction of the snakes, but need not be explained as a reaction to the presence of another species. It may represent compensation for changes in the available niche, *T. radix* seeking out higher light intensities and substrate temperatures to compensate for lower available air temperatures in the sympatric region; *T. sirtalis* seeking out lower light intensities and substrate temperatures to compensate for higher available air temperatures in the sympatric region and for the scarcity of shade normally afforded by the closed marsh and forest of its allopatric habitat.

One of the ways in which this selection could have been accomplished is suggested by the daily profiles of catch per search hour. In the allopatric region, both species showed a roughly bimodal activity pattern with morning and evening peaks. In the sympatric region, however, *T. radix* was most active during mid-afternoon close to the hottest part of the day, and *T. sirtalis* was active earlier in the morning and later in the evening, apparently avoiding the heat of mid-afternoon. This increased difference between the activity patterns of *T. radix* and *T. sirtalis* in the sympatric region was illustrated by univariate comparisons of time to capture, coded to reflect midday activity. The difference in time of capture between *T. radix* and *T. sirtalis* was increased in the sympatric region, but was not great (.05 > P > .01). Multivariate results virtually eliminated the increased importance of this factor in the sympatric region indicating that the activity shift was entirely due to the selection of higher light intensities and substrate temperatures by *T. radix* and lower ones by *T. sirtalis*.

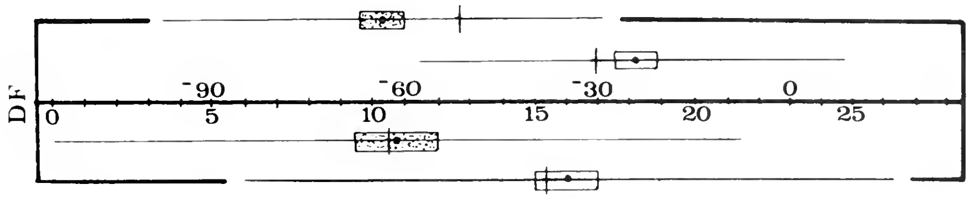

Fig. 3. Location of *T. radix* and *T. sirtalis* on the axes of the discriminant functions (DF) derived from seasonally adjusted data in allopatric and sympatric regions. Symbols and format as in *Fig. 2.*

These changes in selection of light intensity and substrate temperature must represent behavioral adjustments other than those reflected in the daily activity pattern.

MacArthur and Levins (1967) showed that when ecological similarity surpasses a minimal limit, interspecific selective forces act to produce competitive niche displacement. While the relative niche positions of *T. radix* and *T. sirtalis* changed in the sympatric region, there was no net displacement of the niches occupied (Fig. 3). This does not preclude a competitive interaction since there was probably an increased similarity of the available niches. It does, however, suggest that competitive interaction was of minor significance if it occurred at all. The relationship between limiting similarity and resource availability in competitive interactions has been discussed by May (1974), Riebesell (1974) and Pianka. 1974). Schoener (1974) has pointed out that resource availability is an unmeasured variable in most studies of resource partitioning. Measurement of niche separation relative to the available niche breadth was not attempted in the present study due to the difficulty of quantifying an available as opposed to occupied niche with respect to the environmental factors considered.

Thermal Relations.—The higher body temperatures of *T. radix* in the allopatric region (Fig. 4) suggest that this species has a slightly higher preferred temperature than *T. sirtalis.* Such a difference would correlate well with differences in thermal tolerance. *Thamnophis sirtalis* is reported to have a slightly lower minimum critical temperature than *T. radix* (Fitch, 1965). Vincent (1971) found *T. Sirtalis* hibernating at body temperatures as low as -3°C while Bailey (1949) did not find *T. radix* to survive hibernation at temperatures lower than -2°C. While cloacal body temperatures of *T. sirtalis* upon capture were slightly lower than those reported by Fitch (1965) as "preferred", body temperatures of reptiles captured in the field are often found to be lower than preferred temperatures (Licht et al., 1966) due, perhaps, to greater catchability at sub-optimal temperatures.

In spite of the ecological adjustments made by both species in the sympatric region, in apparent compensation for marginal air temperatures, body temperatures became more similar there. This was primarily due to an increase in the body temperature of *T. sirtalis*, which probably indicates that *T. sirtalis* had passed its limit of behavioral thermal adjustment and may explain why it was unable to pene-

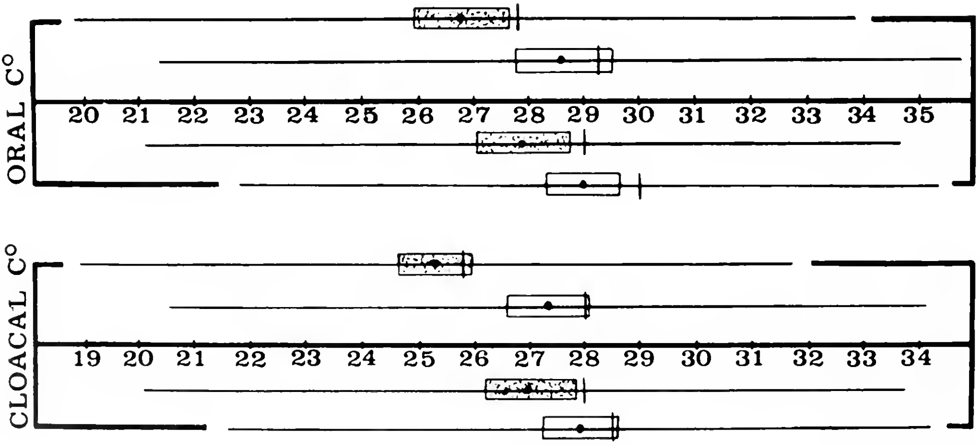

Fig. 4. Oral and cloacal temperatures of *T. radix* and *T. sirtalis* in allopatric and sympatric regions. Symbols and format as in *Fig. 2.*

trate further into the range of *T. radix*. Body temperatures of *T. radix* were not altered appreciably in the sympatric region, and in fact showed a very slight increase in spite of the fact that *T. radix* there was at the northern periphery of its range. *Thamnophis radix*, therefore, had not passed its limit of behavioral thermal adjustment, but was probably at or very close to this limit in the sympatric region. Neither *T. radix* nor *T. sirtalis* would have been able to alter their activity patterns much further since *T. radix* was already concentrating its activity in the hottest part of the day and *T. sirtalis* had virtually eliminated its mid-day activity.

Negative skewness in the frequency distributions of reptilian body temperatures is often reported (Cowles and Bogert, 1944; Brattstrom, 1965). As Heath (1964) points out, although this pattern is often interpreted as indirect evidence for a photophobic reaction at body temperatures higher than the modal one, similar patterns are produced by inanimate objects incapable of movement, and need not be attributed to behavioral thermoregulation. The significance of the pattern in the body temperature distributions of *T. radix* and *T. sirtalis* is, therefore, uncertain.

The oral and cloacal body temperatures of *T. radix* and *T. sirtalis* depended most strongly upon air temperature (Table 3) and next most strongly upon substrate temperature. Fleharty (1967) related cloacal temperatures of *T. elegans, T. cyrtopsis* and *T. rufipunctatus* primarily to substrate temperature and found little effect due to air temperature. However, Fleharty measured air temperature 24 cm above ground level rather than immediately above ground level as in the present study. He measured substrate temperature right at ground level so that it represented the combined effects of air and substrate temperature as measured in the present study. Gregory (pers. comm.) found cloacal temperatures of *T. ordinoides, T. elegans and T. sirtalis pickeringi* to depend strongly upon both air and substrate temperatures; the latter, measured immediately below ground level, exerted the greatest effect.

Oral temperatures of both *T. radix* and *T. sirtalis* depended strongly upon light intensity. While the cloacal temperatures of *T. radix* also depended upon this factor, those of *T. sirtalis* did not. This may be explained by the fact that *T. sirtalis* was often captured on the sedge mat of a closed marsh, with its head above the mat

TABLE 3. Regression equations for dependence of oral and cloacal temperatures on environmental factors [Y = I + (H x Habitat) + (M x Moisture) + (L x Light) + (A x Air Temp.) + (S x Sub. Temp.) + (T x Time)]

	T. radix		*T. sirtalis*	
Y:	Oral	Cloacal	Oral	Cloacal
I	6.941	-1.620	4.420	-0.113
H	0.259	0.222	-1.081**	-1.090**
M	-0.485	-0.525	1.460	3.048**
L	0.626*	0.358*	0.448*	0.073
A	0.448*	0.513*	0.536*	0.635*
S	0.165*	0.164**	0.273*	0.382**
T	-0.239	-0.210	0.029	0.333**

*Partial regression coefficient non-zero (P <.01)
**Partial regression coefficient non-zero and different from that of the other species (P <.01)

and its tail below, shaded from the sun. Light intensity was not measured under the sedge mat.

Oral and cloacal temperatures of *T. sirtalis* were influenced by habitat. The protection from the sun offered the snake by the sedge mat and forest of the closed marsh habitat probably explains this effect.

The direct effect of substrate moisture upon the cloacal temperatures of *T. sirtalis*, other factors being equal, may have been due to relative humidity near the substrate, which was not measured. a direct effect of relative humidity upon body temperatures of reptiles, due to inhibition of evaporative cooling, was suggested by Cowles and Bogert (1944). Relative humidity was probably high under the sedge mat of a closed marsh. Such an effect probably is not completely explained by the habitat factor since there was considerable variability in the moisture of a closed marsh between the edges and the center.

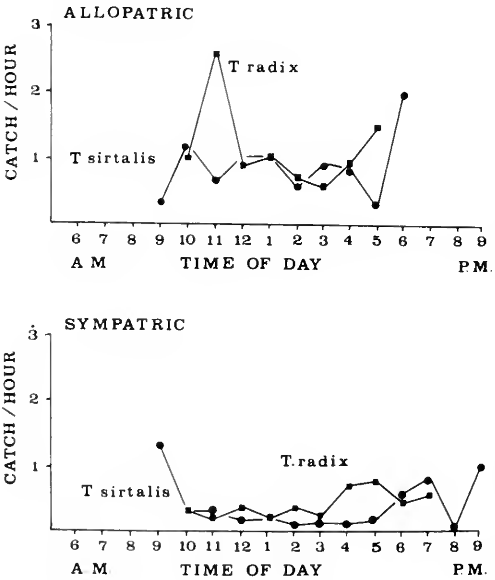

Fig. 5. Profiles of catch per search-hour calculated for hourly intervals throughout the course of the day. Profiles are shown for *T. radix* (solid squares) and *T. sirtalis* (solid circles) in allopatric and sympatric regions.

The direct effect of time of capture, coded as a deviation from mid-day, upon the cloacal temperatures of *T. sirtalis* is difficult to interpret. Diel variations in other measured environmental factors such as light intensity, air temperature and substrate temperature cannot, in a multiple regression, explain an independent effect due to time of capture. Such variations would, in a simple regression, be expected to result in an inverse rather than direct relationship between body temperature and time of capture, with higher body temperatures closer to mid-day. The observed effect of time of capture upon the cloacal temperatures of *T. sirtalis* over and above those produced by variation in other measured factors suggests either the influence of unmeasured environmental factors exhibiting a diel cycle or an intrinsic diel cycle in cloacal temperature.

Activity.—The degree of bimodality in the daily activity pattern of *T. radix* was found by Heckrotte (1962) to be temperature dependent. A similar temperature dependence appears in the daily activity patterns of both *T. radix haydeni* and *T. sirtalis parietalis* (Hart, 1975) and explains the opposite adjustments in activity pattern made by *T. radix* and *T. sirtalis* in the sympatric environment (Fig. 5) and the increased importance of time of capture in discriminating between the niches of *T. radix* and *T. sirtalis* in this region. By becoming most active near mid-day, *T. radix* was able to select higher light intensities and substrate temperatures. By avoiding the heat of mid-day, *T. sirtalis* was able to select lower light intensities and substrate temperatures. Jordan (1967), on the basis of a small sample of snakes from roads within a region of sympatry in Minnesota, similarly found *T. sirtalis* to be active earlier in the morning and later in the evening than *T. radix.*

Competitive Interaction and Density-Dependence.—The primary importance of physical as opposed to biotic factors in the ecology and evolution of temperate zone animals and plants has been stressed by Dobzhansky (1950) and Fischer (1961). Bogert (1949) suggested that this was especially true of northern poikilotherms and noted that stringent thermal requirements might prevent specialization with respect to density-dependent ecological factors. The importance of thermal factors to northern reptiles has been illustrated by Gregory (1977b) who attributed the disappearance of the youngest year class at a communal den of *T. sirtalis* to reproductive failure brought on by a cool, cloudy summer. It is illustrated in the present study by the fact that ecological adjustments made by both *T. radix* and *T. sirtalis* at their range peripheries involved those niche parameters most strongly related to body temperatures. Marked reduction in the relative frequency of *T. sirtalis* captures following spring flooding of many of its dens during the present study further emphasizes the significance of climatic factors in regulating populations of northern reptiles. These factors act independently of density and often catastrophically. The similar feeding habits of *T. radix* and *T. sirtalis* in Manitoba and the lack of evidence for niche displacement between them suggest that density-dependent factors such as competitive interaction are probably not important to northern poikilotherms enduring a harsh continental climate. However, the food partitioning among three *Thamnophis* species on Vancouver Island (Carr and Gregory, 1976; Gregory, 1978) is suggestive of competitive interaction. Such density-dependent factors may be important to northern poikilotherms in maritime regions where the climate is more moderate.

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LITERATURE CITED

Bailey, R.M. 1949. Temperature toleration of garter snakes in hibernation. Ecology 30: 238-242.

Bogert, C.M. 1949. Thermoregulation in reptiles: A factor in evolution. Evol. 3: 195-211.

Brattstrom, B.H. 1965. Body temperatures of reptiles. Amer. Midl. Natur. 73: 376-422.

Carr, C.M. and Gregory, P.T. 1976. Can tongue flicks be used to measure niche sizes? Can. J. Zool. 54: 1389-1394.

Carpenter, C.C. 1952. Comparative ecology of the common garter snake (*Thamnophis sirtalis sirtalis*), the ribbon snake (*Thamnophis sauritus*) and Butler's garter snake (*Thamnophis butleri*) in mixed populations. Ecol. Monogr. 22: 235-258.

Cooley, W.W. and Lohnes, P.R. 1971. Multivariate data analysis. Wiley and Sons Inc., Toronto.

Cowles, R.B. and Bogert, C.M. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. 83: 261-296.

Dobzhansky, T. 1950. Evolution in the tropics. Amer. Sci. 38: 208-221.

Fischer, A.G. 1961. Latitudinal variation in organic diversity. Amer. Sci. 49: 50-74.

Fitch, H.L. 1965. An ecological study of the garter snake *Thamnophis sirtalis*. Univ. Kansas Publ. Mus. Nat. Hist. 15: 493-564.

Fleharty, E.D. 1967. Comparative ecology of *Thamnophis elegans*, *Thamnophis crytopsis* and *Thamnophis rufipunctatus* in New Mexico. Southwest. Natur. 12: 207-230.

Fouquette, M.J. 1954. Food competition among four sympatric species of garter snakes. Texas J. Sci. 6: 172-188.

Green, R.H. 1974. Multivariate niche analysis with temporally varying environmental factors. Ecology 55: 73-83.

Gregory, P.T. and Stewart, K.W. 1975. Long-distance dispersal and feeding strategy of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba. Can. J. Zool. 53: 238-245.

__________. 1977a. Life history observations of three species of snakes in Manitoba. Can. Field Natur. 91: 19-27.

__________. 1977b. Life-history parameters of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in an extreme environment, the Interlake region of Manitoba. Nat. Mus. Canada, Publs. Zool. No. 13, 44 pp.

__________. 1978. Feeding habits and diet overlap of three species of garter snakes (*Thamnophis*) on Vancouver Island. Can. J. Zool. 56: 1967-1974

Hart, D.R. 1975. A quantitative niche comparison of the western plains garter snake (*Thamnophis radix haydeni*) and the red-sided garter snake (*Thamnophis sirtalis parietalis*) in allopatric and sympatric regions of Manitoba's Interlake District. M.Sc. Thesis, University of Manitoba, Winnipeg, Canada.

Heath, J.E. 1964. Reptilian thermoregulation: evaluation of field studies. Science 146: 784-785.

Heckrotte, C. 1962. The effect of the environmental factors in the locomotory activity of the plains garter snake (*Thamnophis radix radix*). An. Behav. 10: 193-207.

Heinselman, M.L. 1963. Forest sites, bog processes and peatland types in the glacial Lake Agassiz region, Minnesota. Ecol. Monogr. 33: 327-374.

Ito, K. *in* Krishnaiah, P.R. (ed.) 1969. Multivariate Analysis II. Academic Press, New York.

Jordan, O.R. 1967. The occurrence of *Thamnophis sirtalis* and *Thamnophis radix* in the prairie-forest ecotone west of Itasca State Park, Minnesota. Herpetologica 23: 303-308.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey.

Licht, P., Dawson, W.R., Shoemaker, V.H. and Main, A.R. 1966. Observations on the thermal relations of Western Australian lizards. Copeia 1966: 97-110.

MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. Amer. Nat. 101: 377-385.

May, R.M. 1974. On the theory of niche overlap. Theor. Pop. Biol. 5: 297-332.

Pianka, E.R. 1974. Niche overlap and diffuse competition. Proc. Nat. Acad. Sci. 71: 2141-2145.

Press, S.J. 1972. Applied multivariate analysis. Holt, Rhinehart and Winston, Inc., New York.

Radforth, N.W. 1964. Prerequisite for design of engineering works on organic terrain – a symposium. Part II – Definitions and terminology. NRC Assoc. Cettes on Soil and Snow Mechanics, Tech. Memo. 81: 24-35.

Riebesell, J.F. 1974. Paradox of enrichment in competitive systems. Ecology 55: 183-187.

Scheffé, H. 1959. The analysis of variance. John Wiley and Sons, New York.

Schoener, T.W. 1974. Competition and the form of habitat shift. Theor. Pop. Biol. 6: 265-308.

Vincent, T. 1971. Resistance to cold stress in the red-sided garter snake *Thamnophis sirtalis parietalis*. M.Sc. Thesis, University of Manitoba, Winnipeg, Canada.

White, M. and Kolb, J.A. 1974. A preliminary study of *Thamnophis* near Sagehen Creek, California. Copeia 1974: 126-136.

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