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A NEW CYPRINID FISH OF THE GENUS *PHOXINUS* (PISCES: CYPRINIFORMES) FROM THE TENNESSEE RIVER DRAINAGE WITH COMMENTS ON RELATIONSHIPS AND BIOGEOGRAPHY

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Abstract.—*Phoxinus tennesseensis* is described from the upper Tennessee River drainage of Tennessee and Virginia. This sexually dimorphic and seasonally brilliantly colored new dace is rare, occurring as localized populations in a few small streams. It is distinguished from the similar *P. oreas* by differences in pigmentation, scale counts, and morphometrics. *Phoxinus tennesseensis* and *P. oreas* are hypothesized to be sister species with *P. cumberlandensis* as their next closest relative. An hypothesis of the biogeographic history of these taxa is advanced.

The small fine-scaled minnows of the genus *Phoxinus* Rafinesque, commonly called in America the redbelly daces, are among the most brilliantly colored of all fishes when spawning. Based on current understanding of cyprinid systematics (Howes 1985:66, Jenkins & Starnes, unpubl. data) *Phoxinus* is the only cyprinid genus native to both Eurasia and North Ameria. It is represented in Eurasia by *Phoxinus phoxinus* and possibly additional forms, and in North America by six species: *P. cumberlandensis, P. eos, P. erythrogaster, P. neogaeus, P. oreas,* and the species described here from the upper Tennessee River drainage in Tennessee and Virginia. All of the North American species with the exception of the relatively recently described *P. cumberlandensis* (Starnes & Starnes, 1978:509) were formerly allocated to the nominal genus *Chrosomus* Rafinesque.

The undescribed species from the Tennessee drainage has been recognized as new by ichthyologists working in the region since the 1960s. Examination of museum specimens revealed a collection made in 1867 from Virginia by Edward D. Cope and an identifiable literature record (Henshall 1889: 31) refers to specimens collected in 1888 from near Chattanooga, Tennessee by Charles Dury (see "Distribution"). These early workers and others who studied fishes from the region failed to recognize the taxon as distinct from *P. erythrogaster* until Carl L. Hubbs identified a series (UMMZ 96851) as *P. oreas.* Ross & Carico (1963:12) regarded specimens from the Pigeon River system as an undescribed subspecies of *P. oreas.* Our study indicates that these records represent an undescribed species.

Recent surveys show that the new minnow is rare, known from several localized populations in generally tiny streams. It has been listed as a species Deemed in Need of Management by the State of Tennessee, and of Special Concern by the Tennessee Heritage Program (Starnes & Etnier 1980:121). It is of Special Concern, but possibly threatened in Virginia (Jenkins & Burkhead, in press).

Methods of counts and measurements generally follow Hubbs & Lagler (1958:19–27) or are self-explanatory. In addition, "scales in longitudinal series" were counted at the level of the incomplete lateral line continuing to the caudal-fin base. "Vertical scale rows" were counted diagonally from the dorsal-fin origin to the anus. Vertebral

counts were made from radiographs with the Weberian apparatus counted as four elements. Proportional measurements are expressed as thousandths of standard length. Population samples used in morphometric comparisons consisted of roughly half adult males and half adult females with gravid females excluded.

Specimens examined are deposited in the following institutions: American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), Cornell University (CU), Eastern Kentucky University (EKU), North Carolina State Museum (NCSM), Northeast Louisiana University (NLU), Roanoke College (RC), Tulane University (TU), University of Alabama (UAIC), Florida State Museum, University of Florida (UF), University of Michigan Museum of Zoology (UMMZ), National Museum of Natural History, Smithsonian Institution (USNM), and University of Tennessee (UT).

Phoxinus tennesseensis, new species
Tennessee dace
Figs. 1a–c, 2b

Chrosomus erythrogaster.—(misidentifications) Cope 1868:241, 245 (Middle Fork Holston system, Va.).—Henshall 1889:31 (Whiteside, Tn.).—Evermann & Hildebrand 1916:443 (Roaring Fork, Greenville, Tn.).—Evermann 1918:339 (Clinch system, Clinton, Tn.).—Fowler 1923:9, 1924:391 (Holston system, Va.).—Fowler 1936:111 (Hiwassee system, Tn.).—Kuhne 1939:fig. 20 (female only, locality unspecified).

Chrosomus oreas subspecies.—Ross & Carico 1963:12 (Pigeon system, Tn.).—Jenkins et al. 1972:48, 98 (Tennessee drainage).

Phoxinus erythrogaster (misidentification).—Hitch & Etnier 1974:84 (Hiwassee system, Tn.).

Phoxinus sp.—Hitch & Etnier 1974:84 (Hiwassee system, Tn).

Phoxinus oreas subspecies.—Starnes & Etnier 1980:121 (range in Tn.).—Starnes & Starnes 1980a:339 (range).—Stauffer et al. 1982:35 (Tennessee drainage).—Starnes & Etnier 1986:347 (Tennessee drainage).

Holotype.—TU 97993, 52.2 mm standard length (SL) tuberculate male, Tennessee, Blount County, Little River system, spring tributary to Reed Creek by unnumbered road 8.0 km E of Walland and Tennessee Route 73, 6 Jun 1976, W. C. Starnes, L. B. Starnes, J. A. Louton.

Paratypes.—ANSP 134735, 12 specimens (21.2–48.0 mm SL), Tennessee, Roane Co., Clinch system, tributary to Bear Creek at Tn. Rt. 95 10 rd. km N Clinch River crossing, 15 Feb 1975.—TU 97994,6 (22.3–49.9), same data as holotype.—TU Osteol. 575, 4 (35.1–47.4) (cleared and stained), same data as ANSP 134735.—UAIC 5230.01, 6 (31.8–40.1), Tennessee, Hawkins Co., Holston system, Terrill Creek at county road 4.9 km SSE Surgoinsville and US Rt. 11W, 29 Apr 1976.—UF 21802, 5 (45.4–58.0), same data as UAIC 5230.01 except 15 May 1975.—UMMZ 198977, 18 (19.4–51.3), Tennessee, Hawkins Co., Holston system, Surgoinsville Creek at county road 1.9 km N US Rt. 11W at Surgoinsville, 30 Nov 1975.—USNM 216212, 15 (19.2–57.9), same data as UMMZ 198977.—USNM 288068, 3 (32.4–44.1), same data as ANSP 134735 except 22 Apr 1980.—UT 44.495, 14 (23.3–49.3), Tennessee, Polk Co., Ocoee-Hiwassee system, Indian Creek above bridge 0.2 km above Parksville Reservoir, 19 Apr 1970.—UT 44.992, 7 (29.0–41.5), same data as ANSP 134735 except 1 Dec 1974.—UT 44.1070, 1 (47.1), Tennessee, Blount Co., Little River system, Reed Creek 100 m below mouth Double Branch, 4.5 air km NE Walland, 13 Apr 1975.

Diagnosis.—*Phoxinus tennesseensis* is distinguished from its congeners except *P. oreas* by its distinctive gut morphology (Starnes & Starnes 1978:fig. 3) and the presence of an interrupted and ventrally decurved lower lateral stripe (Fig. 1a–c). In

Table 1.—Selected meristic and morphometric data (expressed in thousandths of standard length) and results of T-tests between *Phoxinus tennesseensis,* including holotype, pooled from six localities in Tennessee River drainage, and *P. oreas* pooled from New, James, Roanoke-Dan and Neuse river systems.

	P. tennesseensis n = 47 (37–58 mm SL)			*P. oreas* n = 50 (38–52 mm SL)		
	Mean	Range	Holotype	Mean	Range	T-stat.
Scales in longitudinal series	81.0	(67–95)	80	73.7	(64–81)	6.22
Vertical scale rows	31.6	(27–35)	30	30.6	(27–34)	2.49
Predorsal distance	534	(507–580)	532	558	(529–581)	8.33
Dorsal-fin origin–caudal-fin base	495	(453–544)	499	479	(434–516)	4.26
Dorsal-fin origin–occiput	331	(304–360)	334	355	(216–395)	6.65
Prepelvic distance	469	(436–507)	450	466	(444–502)	0.69
Anal-fin origin–caudal-fin base	369	(344–392)	391	360	(320–393)	2.92
Maximum body depth	218	(190–236)	213	247	(217–279)	10.57
Maximum body width	151	(116–168)	152	160	(123–196)	3.03
Least caudal peduncle depth	105	(91–118)	107	119	(98–139)	7.46
Head length	246	(220–266)	238	246	(228–261)	0.69
Head depth	158	(143–173)	156	166	(153–180)	4.81
Head width	126	(110–139)	125	125	(113–142)	0.21
Interorbital distance	086	(76–101)	080	096	(83–104)	0.23
Snout length	072	(60–81)	072	074	(60–84)	2.45
Horizontal orbit diameter	072	(60–81)	068	072	(62–88)	0.23
Upper jaw length	071	(60–81)	065	070	(62–79)	0.97
Dorsal-fin length	099	(160–234)	170	210	(156–248)	3.32
Anal-fin length	179	(153–198)	180	194	(157–228)	4.92
Pectoral-fin length	183	(146–223)	189	181	(163–207)	0.56
Pelvic-fin length	146	(104–178)	162	158	(127–187)	3.54

nuptial males, the black chin, isthmus and anterior breast, and red on the lower one-half of the opercle further distinguish these two species from congeners. *Phoxinus tennesseensis* is distinguished from the similar *P. oreas* by smaller dark dorsolateral markings, which when maximally developed, consist of specks generally smaller than pupil versus many blotches much larger than pupil in *oreas* (Fig. 1a, d); also distinguished by the typical presence of a well-developed upper black lateral stripe in adults (usually lacking in *oreas*), red immediately below lower lateral stripe on urosome of nuptial males (silver or gold stripe between lower black stripe and red venter in *oreas*), and the incomplete series of infraorbital bones in *tennesseensis* versus the complete series in *oreas* (Fig. 2). The species are further distinguished by smaller scales [mean scales in longitudinal series 81.0 (67–95) in *tennesseensis* vs. 73.7 (64–81) in *oreas*], less robust head and body [mean body depth 218 (190–236) vs. 247 (217–279)], and more anteriorly positioned dorsal fin [mean predorsal distance 534 (507–580) vs. 558 (529–581)].

Description.—Lateral profile of body evident in Fig. 1a–c. Meristic and morphometric data for holotype and paratypes summarized in Table 1. Ontogenetic variation evident in several morphometric values (see "Variation"). Maximum known standard length 60.0 mm. Body of juveniles terete to elliptical in cross-sectional profile, deeper and more parallel sided in adults. Dorsum of head nearly flat. Eye with slight curvature over top of head. Snout broadly pointed. Mouth subterminal and slightly upturned. Dorsal-fin origin above or posterior to pelvic-fin origin, its relative position sexually dimorphic, inserting more anteriorly in males (mean predorsal distance 527 vs. 540 in females). Fins with broadly

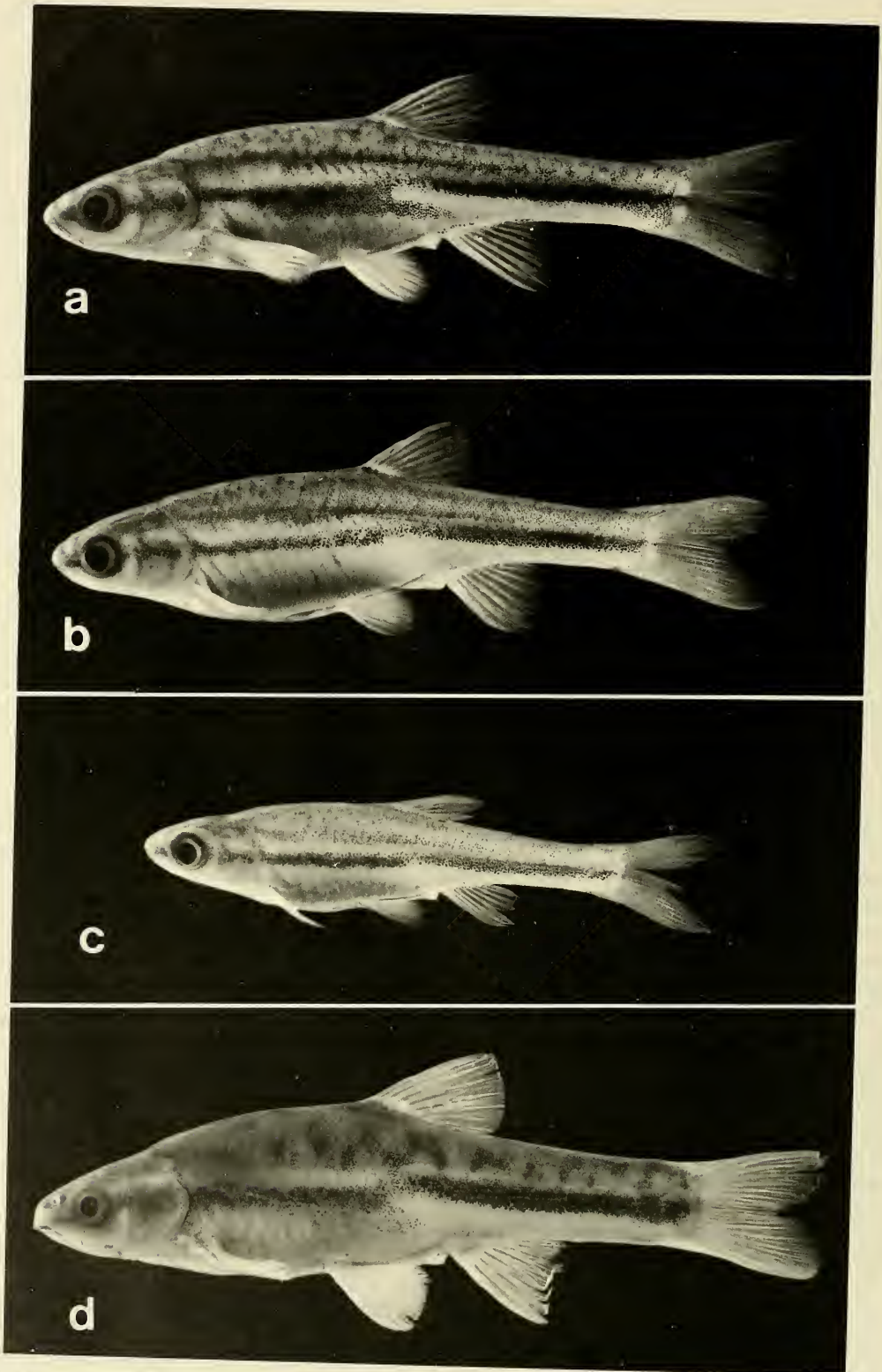

Fig. 1. a–c, *Phoxinus tennesseensis,* from top, 44.2 mm SL male, 42.0 mm SL female, 32.3 mm SL juvenile, all USNM 288068; d, *Phoxinus oreas,* 52.0 mm SL male, USNM 288066.

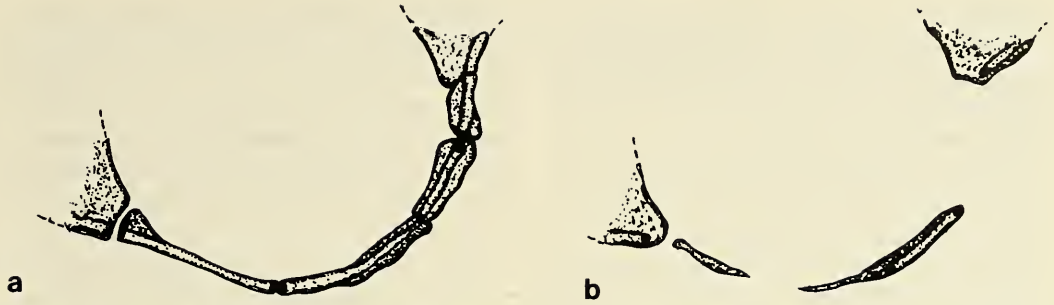

Fig. 2. Infraorbital bones of a, *Phoxinus oreas* (UT 44.1212); b, *Phoxinus tennesseensis* (TU Osteol. 575).

rounded margins. Some fins exhibiting barely significant sexual dimorphism, with dorsal, pectoral and pelvic fins averaging longer in males (mean lengths 202 vs. 195, 187 vs. 176, 150 vs. 139 respectively). No appreciable sexual dimorphism in other morphometric values.

Urogenital papilla of female with pronounced ventromedial ridge; ridge absent in males. Gut long, with about four loops lying more or less transversely (Starnes & Starnes 1978:fig. 3b).

Pharyngeal arches with lateral shelf open, well fenestrated. Each arch with single row of five long and laterally compressed teeth. Grinding surfaces of upper three teeth elongate, with lateral ridges and fine crenulations and slightly hooked at tips. Fourth tooth slightly hooked with reduced grinding surface. Fifth (ventral) tooth bluntly pointed.

Infraorbital series greatly reduced (Fig. 2b). Second and third infraorbitals reduced to narrow remnants, fourth and fifth absent. Infraorbital canal variously interrupted, with 17 to 19 external pores. Supratemporal canal broadly interrupted at midline of nape, pore formula 2-2, 2-3, or 3-3. Supratemporal canal not joined to postocular commissure and usually interrupted above orbit and posterodorsad of nares; total pores usually 8. Preoperculomandibular canal broadly interrupted at mandibular articulation, total pores usually 3 + 6.

Scales cycloid, very fine, covering entire body, absent from head. Scales of breast and belly embedded in flesh, difficult to detect. Scales of remainder of body less deeply embedded in flesh, resulting in very slippery texture and characteristic sheen. Imbrication of scales increasing anteriorly. Scale counts exhibiting geographic variation (see "Variation") and moderately variable within populations. Scales in longitudinal series 67–95 (mean 81.0). Vertical scale rows 27–35 (31.6). Lateral line poorly developed or absent, variable within populations. Pored lateral-line scales 0–33, occasionally interrupted.

Principal dorsal-fin rays 8; anal-fin rays modally 7 (6–8); pectoral-fin rays modally 15 (13–17); pelvic-fin rays modally 8 (6–8); principal caudal rays 19, rarely 18. Total vertebrae (15 specimens) 38–39, 19 precaudal + 19 caudal, or 19 + 20, or 20 + 19. Total gill rakers on first arch usually 11–13.

Breeding tubercles in both sexes on head and entire body except belly, and on rays of all fins except caudal; most prominent in males. Patterns of tuberculation and sexual dimorphism in tubercle development identical to those described in detail for *P. cumberlandensis* by Starnes & Starnes (1978: 512) and generally for *P. oreas* by Raney (1947:128). As in those species, *P. tennesseensis* has uniconic tubercles on head region. Scales on much of body with multiconic tubercles, best developed on scales of posterior portion of body, giving scales ctenoid-like texture. Males have 8 or 9 trans-

verse rows of characteristic comb-like tubercles on each side of breast anterior to interpectoral area, and rows of strong uniserial tubercles on dorsal surfaces of second to fifth pectoral-fin rays.

Color in preservative.—Coloration variable with age, sex, and reproductive state. Darker coloration subdued in young and variable in adults, becoming boldest during spawning, maximally jet black in some males. Side with 2 parallel black stripes, lower interrupted below dorsal fin. Lower stripe relatively broad; posterior portion at mid-height of urosome straight or deflected slightly upward beneath dorsal fin; anterior portion deflected ventrally and variously developed toward anal fin base (Fig. 1a–c), at maximum development extending along base in adult males. Lower stripe continuing forward onto head, and may be well developed on opercle, preopercle, iris, and preorbital area but not on tip of snout. Upper lateral stripe narrow, about one-third width of lower, tapered posteriorly. Upper stripe usually persistent in adults anteriorly, occasionally becoming interrupted, and developed on urosome from above anal fin to hypural area, often represented by broken line posteriorly.

Portion of head and body dorsad of lower lateral stripe with moderately dense melanophore fields; belly and breast (except in nuptial males) immaculate except for few melanophores about pectoral-fin base. Scattered melanophores along anal-fin base and ventrally on caudal peduncle. Patches of melanophores forming black specks on top of head and dorsum of body in some larger individuals (Fig. 1a), particularly nuptial males, almost always smaller than pupil diameter. Middorsal streak usually well developed anterior and posterior to dorsal fin. Lips dusky in specimens of all sizes, becoming intense black in nuptial males. Lip pigmentation coincident with presence of jet black on underside of head from lips to interpectoral area. Melanophores aligned along margins of all dorsal-fin rays, anterior 4 or 5 anal-fin rays, anterior 7 or 8 pectoral-fin rays, and anterior 2 or 3 pelvic-fin rays. Males with black epibasal streak spanning anterior 4 or 5 dorsal-fin rays and membranes. Peritoneum very dusky to black, visible through body wall after preservation.

Life coloration.—In addition to dark pigmentation described above, juveniles and nonbreeding adults with head and body olive to tan dorsal to upper lateral stripe anteriorly and lower lateral stripe posteriorly. Area between lateral stripes anteriorly, and all area below lower lateral stripe on head and body silvery white. Red coloration best developed during breeding season but may be present to various degrees at any time of year and (based on aquarium observations) is rapidly changeable in response to various stimuli.

Maximum development of nuptial coloration occurs in spawning males as follows: dark markings described above jet black. Bright scarlet red covers ventral portion of body below lower lateral stripe from interpectoral area to base of caudal fin (except for black, and for silvery patches). Oblique red slash just behind upper opercle. Red laterally on snout just above upper lip, on lower half of opercle, and forming a broad stripe on upper portion of opercle just above lower black lateral stripe. Red basal band present on rays and membranes of dorsal fin below black epibasal streak. Red may be present on bases of pelvic and anal fins and is present on central caudal fin base, extending onto rays. All fins and iris bright lemon yellow. Dorsum of head and body and iris olive, tan or golden. Brilliant metallic silvery-white patches on lower portion of preopercle, suborbital area, upper one-fifth of opercle and preopercle, areas surrounding bases of pectoral and pelvic fins, and at origin of dorsal and sometimes anal fins. Two vertically aligned and vertically elongate white patches may be present at

caudal fin base. Body between lateral stripes dull white or silvery, occasionally slight yellowish.

Moderately colored spawning males with less intense or diffuse red, dusky instead of black dark markings, and pale yellowish fins. Nuptial females typically lacking red and with yellow in fins and silver patches at fin bases subdued. At peak, females approximate moderately colored males.

Variation.—Phoxinus tennesseensis exhibits both ontogenetic and geographic variation. Ontogenetic analysis is based on shape changes in 52 specimens ranging 20.3–58.0 mm SL. Juveniles of *P. tennesseensis* have relatively larger heads with respect to standard length than adults. This is manifested by marked negative allometry in both head length and width and related submeasurements including interorbital distance, snout length, orbit diameter, and upper jaw length relative to standard length. The proportions of the submeasurements relative to head length or width do not change appreciably with ontogeny indicating relatively isometric growth in the head region. There is slight negative allometry in body width in concert with head width as maturing dace become less terete and more elliptical to almost parallel-sided in cross-sectional profile. Slight negative allometry occurs in caudal peduncle depth. Positive allometry is found only in prepelvic distance, indicating a relative posterior shift in the insertion of the pelvic fins with maturity. Juveniles have relatively greater dorsal-, and anal- and pectoral-fin lengths.

There is no evidence of geographic variation in morphometric proportions, pigmentation, or meristic characters other than scale counts. There is considerable clinal variation in scale counts of *P. tennesseensis,* the numbers increasing in downstream fashion from headwaters of the Tennessee drainage downstream to the Hiwassee system (Fig. 3). Specimens from the upper Holston system in Virginia (RC-REJ 667) average 75.6 (67–84) scales in longitudinal series. Proceeding downstream in the Tennessee drainage, a series from the lower Holston system (USNM 216212) averages 80.0 (75–86); lower Clinch system (ANSP 134735) 86.9 (77–95); Hiwassee system (UT 44.495) 87.0 (79–94). Numbers of vertical scale rows follow a somewhat similar trend averaging 30.6, 33.4, 32.8 and 34.0 respectively. The extent of development of pored lateral-line scales does not seem to vary in a geographic pattern but rather is highly variable within populations.

Comparisons.—Phoxinus tennesseensis is phenetically very similar to *P. oreas,* a native of several central Atlantic slope drainages and the New drainage in North Carolina, Virginia, and West Virginia. Despite this similarity (Fig. 1a, d), *P. tennesseensis* differs significantly from *P. oreas* in aspects of meristics, morphometrics, and pigmentation. Table 1 lists meristic and morphometric data for adults and the results of statistical comparisons using T-tests. *Phoxinus tennesseensis* has smaller scales on the average than *P. oreas,* having much higher average counts for scales in a longitudinal series and averaging slightly higher in vertical scale rows. Based on T-values, there are highly significant differences in predorsal, dorsal-fin origin to occiput, and dorsal-fin origin to caudal-fin base distances. These reflect more posterior insertion of the dorsal fin of *P. oreas* relative to that of *P. tennesseensis. Phoxinus tennesseensis* is distinctly less robust than *P. oreas,* with this reflected in the highly significant differences in head, body, and caudal peduncle depths, and the marginally significant difference in body width. *Phoxinus oreas* has a significantly broader interorbital distance, more dorsally flattened head, and a more declivous snout that *P. tennesseensis,* especially as adults. All fins except the pectorals are relatively shorter in *P. tennesseensis,* with significaant differences in dorsal-, anal-, and pelvic-fin lengths.

Phoxinus oreas has a complete series of infraorbital bones (Fig. 2a) and the sensory canal system in these bones is often complete with 15 external pores modally. The infraorbital series is degenerate in *P. tennesseensis* (Fig. 2b) with the fourth and fifth bones lacking and the second and third reduced. The infraorbital canal in that species is variously interrupted in the nonossified interspaces and has 17 to 19 total external pores.

When maximally developed, particularly in nuptial males, the black dorsolateral pigmentation of adult *oreas* consists of blotches usually much larger than the pupil (Fig. 1d) while that of *tennesseensis* is comprised of specks virtually always smaller than the pupil (Fig. 1a). The upper lateral stripe possessed by juveniles of both species generally persists into maturity in *tennesseensis,* though it may have minor interruptions. In *oreas* this stripe breaks up into a series of blotches or disappears altogether. The red on the ventral portion of the urosome of *tennesseensis* is essentially contiguous with the lower black lateral stripe, but in *oreas* is separated from that stripe by a silvery or golden stripe about equal in width to the black stripe.

The aforementioned clinal scale counts of *P. tennesseensis* (see "Variation"), with lower counts in headwater populations of the Tennessee River drainage (upper Holston system) approaching those of *oreas* in the adjacent New River drainage populations, raises a question of possible intergradation. However, the lack of intermediacy in morphometric attributes or coloration in the upper Holston populations is not congruent with such a possibility. *Phoxinus tennesseensis* is thus recognized as a species.

Phoxinus tennesseensis apparently has much narrower habitat tolerances than *oreas.* The latter is common in both first order and larger streams (to 10 m wide), occurs in both sheltered and more open waters, and occurs extensively in the Blue Ridge which is largely avoided by *tennesseensis.*

Young specimens of *P. tennesseensis,* lacking dorsolateral speckling and ventroflexure of the lower lateral stripe (Fig. 1c), are quite similar in appearance to and have been confused with young of the southern redbelly dace, *P. erythrogaster,* which also occurs allopatrically in the Tennessee drainage. The slight narrowing and incipient break in the lower lateral stripe beneath the dorsal fin in juvenile *tennesseensis* serves to distinguish them from *erythrogaster* which has this stripe uniformly straight throughout life.

Distribution.—*Phoxinus tennesseensis* occurs as highly localized populations in small streams of the Ridge and Valley physiographic province portion of much of the upper Tennessee River drainage in Virginia and Tennessee (Fig. 3, and Starnes & Starnes 1980a:339). While it occurs in several localities near the interface of the Ridge and Valley with the Blue Ridge and Cumberland Plateau provinces, it does not penetrate far into either of the latter two. Surveys of the Clinch-Powell system, a major headwater arm of the Tennessee drainage in the Ridge and Valley province, have failed to reveal the presence of any populations except in the lower reaches. The southwestern-most locality for *P. tennesseensis,* a small unnamed tributary at Whiteside, Marion County, Tennessee, is based on Henshall (1889:31) who clearly described nuptial coloration in this species in specimens collected in 1888 which are no longer extant. This locality has been altered by highway construction and the population is apparently extirpated. No other records are known in the Tennessee drainage downstream of the Hiwassee River system despite relatively thorough collecting.

Populations are known or were formerly known from 28 small streams, several of which, including the type locality, may now be extirpated. Such a distributional pattern may be indicative of relictual populations surviving natural processes of widespread extirpation over the millennia, but humans have had observable impacts on several populations.

Several records of *Phoxinus* from the up-

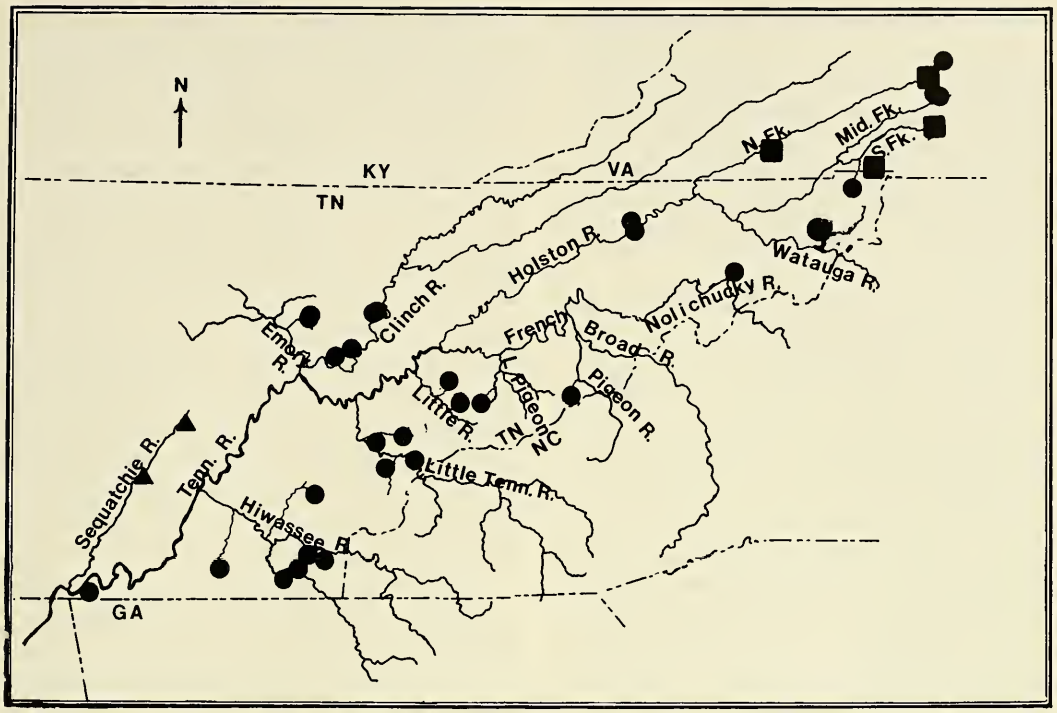

Fig. 3. Upper Tennessee River drainage showing distribution of *Phoxinus tennesseensis* (circles), putative introduced populations of *P. oreas* (squares), and proximate populations of *P. erythrogaster* (triangles).

per Tennessee drainage in Virginia (Fig. 3) do not represent *P. tennesseensis* but rather probable introductions of the similar *P. oreas* [see "Material examined" and Ross & Carico (1963:9) for localities], a species frequently seined for bait in Virginia and occasionally introduced extralimital to its native range (Jenkins & Burkhead, in press). Such introductions are noted as potential sources of confusion to future studies of distribution in these species.

Phoxinus tennesseensis has been confused in the past, particularly as juveniles, with *P. erythrogaster,* also native to the Tennessee drainage. Their distributional relationship is apparently allopatric, with *erythrogaster* occurring mainly to the west of *tennesseensis* in the Highland Rim province (Starnes & Starnes 1980b:337). Two populations of *erythrogaster* in the Sequatchie system (Fig. 3) may represent introductions from the adjacent Cumberland drainage where it is common. Two records of *erythrogaster* from within the general range of *tennesseensis* are rejected as invalid. A series of *erythrogaster* putatively taken from the Emory system in 1952 (CU 30680) is among former Tennessee Game and Fish Commission collections deposited at Cornell. A recent survey of the locality, Crab Orchard Creek, Morgan County, Tennessee, revealed no *Phoxinus* population or likely physical habitat and thus transposition of data is suspected. Equally suspect is a collection purportedly from the upper Clinch-Powell system (Indian Creek, Lee Co., Virginia) which also contains the darter *Etheostoma kennicotti* (ANSP 83177). Neither this species nor *P. erythrogaster* were found in the region in an extensive survey (Masnik 1974:126–127); they co-occur regularly only in the Cumberland and lower Tennessee drainages.

Gilbert's (1891:147) record of "*Chrosomus erythrogaster oreas*" from the Cypress Creek system in northwestern Alabama

raised a question of the possible occurrence of *tennesseensis* in that region. It is puzzling to note that Gilbert's specimens (USNM 36163) are typically pigmented *P. erythrogaster,* though he described them as having an interrupted lateral stripe like that of *tennesseensis* and erroneously regarded them as intergrades between *P. erythrogaster* and *P. oreas.*

Habitat and biology.—*Phoxinus tennesseensis* occurs primarily in first order spring-fed streams of the Ridge and Valley limestone region, which range from less than a meter to two meters in width in faster flowing reaches. Specimens (UT 44.736) from lower Doe Creek, Johnson County, Tennessee, a large trout stream just above a reservoir, probably represent a bait-bucket introduction. Typical habitat streams are of relatively moderate gradient and well shaded by riparian growth or woodlands, thus remaining cool year-around with water temperatures seldom exceeding 22°C or so. Dace are not generally found in close proximity to spring sources but rather are much more common a few hundred meters downstream where they inhabit sluggish pool areas with substrates of fine gravel, sand and silt. Schools or small groups of dace congregate near cover of debris and undercut banks. Fish faunas of streams inhabited by *P. tennesseensis* are not diverse. The most common fish associates are the cyprinids *Campostoma anomalum, Notropis chrysocephalus, N. telescopus, Rhinichthys atratulus,* and *Semotilus atromaculatus* and, in the lower Clinch River system, *Notropis ardens.*

We have not observed actual spawning by Tennessee dace but an aggregation of males in spawning condition was observed in shallow water (8–10 cm depth) over clean, fine-gravel substrate at the head of a small riffle during mid-May at the type locality. This activity is similar to behavior reported for closely related congeners *Phoxinus oreas* (Raney 1947:127) and *P. cumberlandensis* (Starnes & Starnes 1981:366). Both of those species often spawn communally over the nests of gravel-nest-building cyprinids such as *Campostoma, Nocomis,* and *Semotilus.* Both *Campostoma* and *Semotilus* occur in small streams occupied by *P. tennesseensis* but mature adults of the nest-builders are more common in larger streams. Paucity of clean gravel substrates due to siltation stemming from human activities may account in part for the present extremely localized nature of Tennessee dace populations. Under such conditions it was hypothesized that the related *P. cumberlandensis* becomes dependant on nest-building cyprinids for assured purgation of spawning substrate (Starnes & Starnes 1981:367), an opportunity which may not usually be afforded to Tennessee dace.

Contents of intestinal tracts examined and similarity in gut morphology suggest that the diet of *P. tennesseensis* is similar to that of *P. oreas* and *P. cumberlandensis* (Flemer & Woolcott 1966:85, Starnes & Starnes 1978:362), consisting largely of organic detritus, algae, and diatoms. Observed size classes in collections correspond closely to those reported for *P. cumberlandensis* (Starnes & Starnes 1981:368) which has a lifespan of three years and reaches sexual maturity in one year.

Relationships.—Within the genus *Phoxinus, P. tennesseensis* shares with the phenetically very similar and geographically proximate *P. oreas* three unique and presumably derived pigmentation attributes: the interrupted and ventrally decurved lower black lateral stripe; black pigment on the chin, isthmus, and prepectoral area of nuptial males; and red pigment on the lower operculum. *Phoxinus tennesseensis* and *P. oreas* are thus hypothesized to be sister species. *Phoxinus cumberlandensis,* of the upper Cumberland River drainage in Kentucky and Tennessee, shares with these two species several conditions that are hypothesized to be shared derived features within the context of a hypothesized monophyletic grouping comprising the genus *Phoxinus,*

compared to a broad selection of North American and Eurasian cyprinids. These include the configuration of the elongate, coiled gut (generalized condition shorter, fewer bends), the distinctly bilobed posterior configuration of the opercular bone (plesiomorphic condition broadly rounded) (Starnes & Starnes 1978:figs. 2, 3), the presence of random dorsolateral speckling or blotching (vs. rows of spots or plain), and the presence of two shagreen patches of breeding tubercles on the opercle (vs. single continuous patch if present). *Phoxinus cumberlandensis* is thus hypothesized to be the sister species to the phyletic line including *P. oreas* and *tennesseensis*. The results of electrophoretic studies on *Phoxinus* allozymes reported by Joswiak (1980:27) tend to support this hypothesis.

The most tenable biogeographic scenario implicit in the relationships hypothesized above, together with present-day distribution of the involved taxa, places the common ancestor to *P. cumberlandensis* and *P. oreas* + *tennesseensis* in eastern portions of the preglacial Teays River drainage [the fish fauna of the upper Cumberland River above Cumberland Falls is hypothesized to be derived largely or wholly from former Teays tributaries to the north (Starnes & Etnier 1986:339)]. Vicariance between *P. tennesseensis* and *P. oreas* was perhaps effected by capture of an upper Teays (New River) tributary by an upper Tennessee River (Holston River) tributary. A sweepstakes dispersal from the New River into the Holston through the karst region interlying the two drainages is an alternative hypothesis. *Phoxinus oreas* has subsequently dispersed into several Atlantic slope tributaries east of New River. Thus *P. cumberlandensis, P. oreas,* and *P. tennesseensis* are hypothesized to be relictual manifestations of a precursory form formerly widespread in the upper Teays region.

Etymology.—A shortened combination of "Tennessee" and the Latin suffix "-ensis," denoting place, in reference to the Tennessee River drainage to which this species is endemic.

Other material examined.—*Phoxinus tennesseensis:* Holston River system, Virginia: ANSP 22112-13, 2, Smyth Co., Bear Creek, trib. Mid. Fk. Holston River, 1867.—RC JRS 1, 1, Smyth Co., Bear Creek 12.1 air km NE center Marion, 1972.—RC JRS 2, 5, Smyth Co., Bear Creek 12.0 air km NE center of Marion, 1972.—RC REJ 666, 8, Smyth Co., Bear Creek at end Rt. 694, 2.7 rd. km ENE jct. rts. 622–694, 1974.—RC REJ 667, 71, Smyth Co., Bear Creek along Rt. 694, 1.5 km ENE jct. rts. 622–694, 1974.—TU 97995, 10, and TU Osteol. 576, 4 (cleared and stained), same as RC REJ 667.—RC TVA 43, 1, Middle Fork Holston River 0.3 km above Bear Creek, 1973.—RC MES 23, 12, Bland Co., Lick Creek (trib. North Fork Holston River) above uppermost Rt. 625 bridge, 3.1 air km N Ceres, 1973.—RC REJ 752, 2, Bland Co., Lick Creek off Rt. 625, 2.7 km above uppermost bridge, 2.9 air km NNW Ceres, 1976.—Tennessee: UT 44.736, 2, Johnson Co., Doe Creek, trib. to Watauga River, at Doeville, 1973.—UT 44.1700, 3, Johnson Co., Beaverdam Creek, trib. to South Fork Holston River, on US 421 7.5 air mi. NW Mountain City, 1978.—UT 44.2693, 1, same as previous except 1982. Nolichucky River system, Tennessee: UT 44.653, 1, Washington Co., tributary to Cherokee Creek at Greenwood Drive 4.7 km from jct. Brush Creek Road, 1972. Pigeon River system, Tennessee: AMNH 62947, Cocke Co., tributary to Cosby Creek 0.3 km above National Park boundary, 1960. Little River system, Tennessee: UMMZ 96851, 59, Blount Co., headwaters Reed Creek, E Walland, 1928. Little Pigeon River system, Tennessee: NLU 16066, 3, Sevier Co., Cove Creek on Covemont Church Road in Wear Cove SW Sevierville, 1967. Little Tennessee River system, Tennessee: NLU 9593, 3, Blount Co., tributary to Fourmile Creek at US Rt. 129 25.8 km S of Maryville, 1968.—TU 25660, 2, Blount Co., tributary to Fourmile Creek

at jct. rts. 72–129 4.8 km NW Tallassee, 1961.—UMMZ 183714, 1, Blount Co., Tabcat Creek near Calderwood, 1957.—UT 44.98, 2, Monroe Co., Caney Branch (trib. Citico Creek), 1967. Clinch River system, Tennessee: CU 19129, 10 (combined from 3 localities), Anderson Co., Harness Creek 1.0 km W Clinton; tributary to Brushy Fork 6.9 km W Clinton; and Little Cow Creek 1.8 km N Oliver Springs, all 1950.—UT 44.765, 49, Roane Co., tributary to Bear Creek at Tn. Rt. 95 10 rd. km N Clinch River, 1971. Emory River system, Tennessee: UT 44.1098, 3, Morgan Co., Beech Fork Creek at Tn. Rt. 62 9.7 km E Wartburg, 1974. Hiwassee River system, Tennessee: ANSP 54464-67, 4, Bradley Co., Candies Creek near Cleveland, 1930.—EKU 797, 30, Polk Co., Smith Creek at Co. Rt. 4314 8.2 air km NNW Harbuck, 1976.—UT 44.496, 7, Polk Co., Indian Creek above bridge 0.2 km above Parksville Reservoir, 1970.—UT 44.575, 2, McMinn Co., Chestuee Creek at Nonaburg, 1970.—UT 44.589, 2, Polk Co., Madden Branch near Parksville Reservoir, and 12 (fin-clipped), Indian Creek near Parksville Reservoir, 1970.

Phoxinus erythrogaster: Sequatchie River system, Tennessee: UT 44.1165, 27. Tennessee River drainage, Alabama: UAIC 1965, 13; UAIC 1982, 26; UAIC 4805.03, 12; UAIC 4821.06, 2; USNM 36161, 6. Locality uncertain: ANSP 83178, 49; CU 30680, 1.

Phoxinus oreas: James River drainage, Virginia: UAIC 1048, 3; UAIC 1050, 2; UAIC 1681, 21; UAIC 2568, 1; UT 44.679, 7. Roanoke-Dan river system, Virginia: UAIC 1435, 6; UAIC 1680, 133; UAIC 3050, 26; UT 44.202, 32, UT 44.207, 26; UT 44.526, 45; UT 44.729, 7; UT 44.1212, 5 (cleared and stained). Neuse river system, North Carolina: NCSM 3775, 4; NCSM 4857, 21. New river system, Virginia: USNM 288066, 1; UT 44.239, 5; UT 44.509, 9; UT 44.730, 7; UT 44.1077, 32; UT 44.1213, 3 (cleared and stained). Tennessee River drainage, Virginia: AMNH 62748, 5, Smyth Co., Comers Creek (trib. South Fork Holston River), 1966; RC REJ 980, 1, Washington Co., Whitetop Laurel Creek (trib. South Fork Holston River), 1983; USNM 288067, 1, Bland Co., confluence Lick and Lynn Camp creeks (North Fork Holston system), 1978.

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