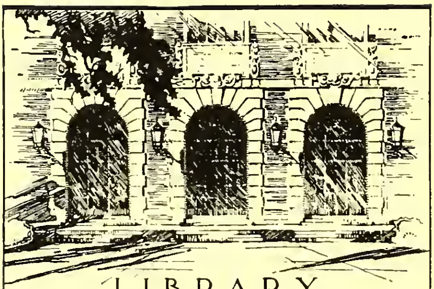
SYSTEMATICS OF THE SALAMANDER GENUS *GYRINOPHILUS*



SYSTEMATICS OF THE SALAMANDER GENUS *GYRINOPHILUS*

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THE SALAMANDER GENUS
GYRINOPHILUS

RONALD A. BRANDON

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35

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INTRODUCTION

Gyrinophilus is an eastern North American genus of the family Plethodontidae containing salamanders reaching an adult length of 100–130 mm (snout-vent) (Figs. 1–2). These pinkish, reddish, or brownish salamanders seem to be restricted ecologically to springs, caves, and small, rapidly flowing streams. They are essentially aquatic, have a long larval period (2–3 years), and as adults are seldom found far from springs or stream banks. Of the two included species, one is entirely restricted to caves (troglobitic) while the other is typically found in surface springs and streams (epigean), although there are numerous records of cavernicolous populations of the latter in cave regions.

The earliest description of a salamander presently placed in the genus *Gyrinophilus* appeared in 1827. Preserved specimens have been accumulating in museum, university, and personal collections at a progressively increasing rate for the past 139 years. A critical taxonomic study of the entire genus has not appeared since Dunn's monograph (1926) of the family Plethodontidae, although most collections from taxonomically critical areas have been made since 1930. Since then the only fairly comprehensive report (Mittleman, 1942) introduced many problems and misunderstandings.

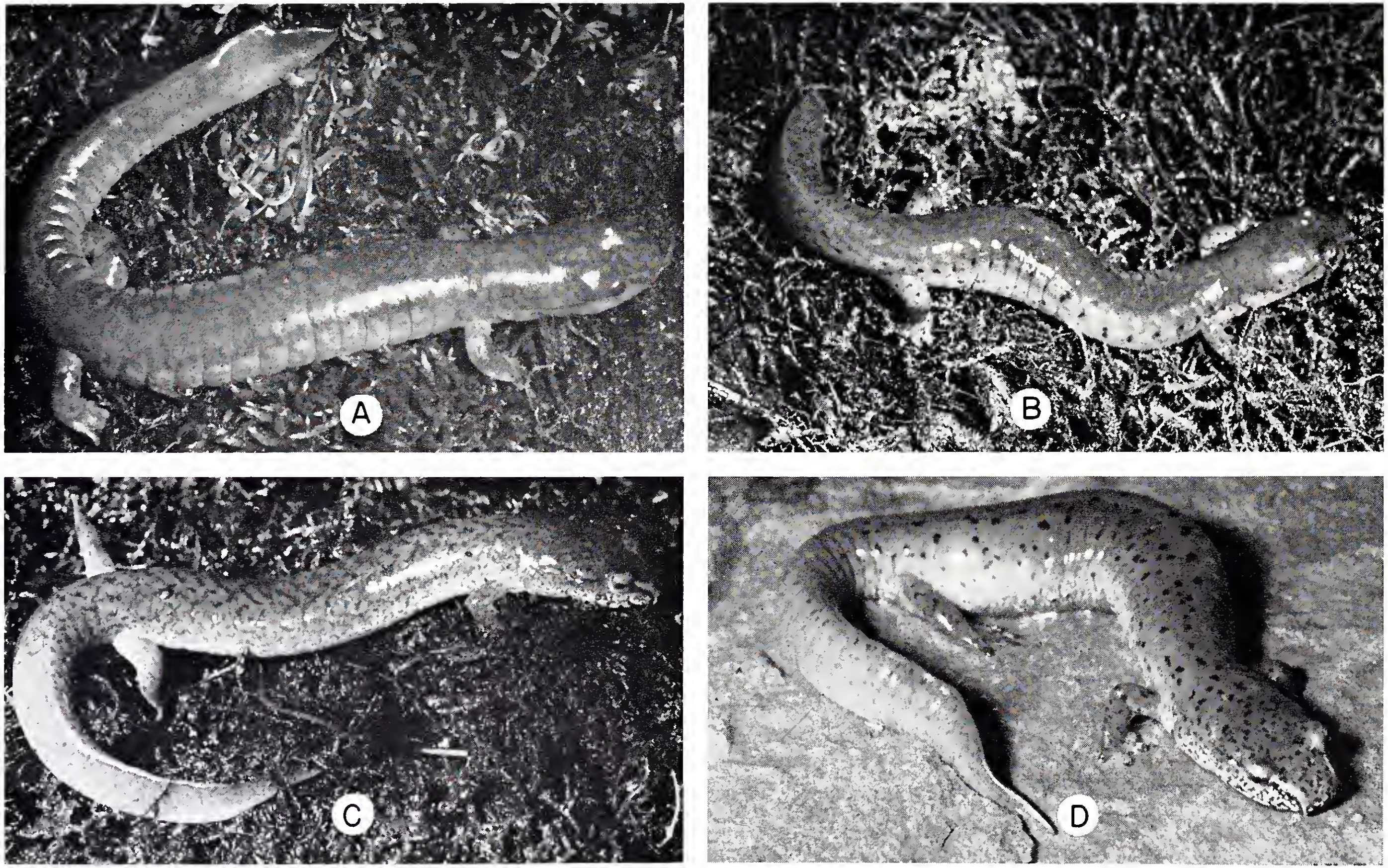
Three factors make this an opportune time to review the genus systematically: (1) the existence of numerous published reports and identifications (many questionable) of *Gyrinophilus*, (2) numerous conflicting opinions concerning the taxonomic status of the described forms and of the genus itself, and (3) the existence of many excellent collections of preserved specimens from throughout the known range of the genus. The present study, then, involves a complete re-examination of specimens and literature in an attempt to interpret and integrate existing material into a factual taxonomic understanding of this genus of plethodontid salamanders.

The numerous reports of the distribution of *Gyrinophilus* appearing prior to 1926 as cited by Dunn, and those reporting specimens from New York listed by Bishop (1941) are not repeated here. The following articles reporting *Gyrinophilus* from the several regions supplement those given by Dunn and Bishop: Alabama (Chermock, 1952a, 1952b; Lazell and Brandon, 1962; Thurow, 1954, 1955); Canada (Bleakney, 1954; Hall, 1947; Logier, 1952; Logier and Toner, 1955); Georgia (Martof, 1955; Martof and Humphries, 1955; Neill, 1941, 1947, 1957); Kentucky (Barbour, 1953; Burt, 1933; Dury and Williams, 1933; Walker and Weller, 1932; Welter and Carr, 1939); Maine (Fowler and Sutcliffe, 1952); Maryland (Fowler, 1944; McCauley and East, 1940); Mississippi (Ferguson, 1961); North Carolina (Hairston, 1947, 1949; King, 1939); Ohio (Kirtland, 1838; Seibert and Brandon, 1960; Smith, 1882; Walker and Weller, 1932; Wilcox, 1891); Pennsylvania (Burger, 1933; Heilman, 1951; Mohr, 1943; Netting, 1928; Netting and Wilson, 1940); South Carolina (Pickens, 1927); Tennessee (Brandon, 1965; Gentry, 1955; Hay, 1903; Ives, 1927; King, 1939; Sinclair, 1950); Virginia (Hoffman and Kleinpeter, 1948a, 1948b; Hutchison, 1956; Netting, 1932; Newman, 1954; Organ, 1961b); West Virginia (Bond, 1931; Green, 1941, 1942; Llewellyn, 1940; Netting, 1933; Reese, 1932; Richmond and Boggess, 1938; Wilson and Friddle, 1950).

Reports which directly or indirectly deal with aspects of *Gyrinophilus* other than its distribution are as follows: anatomy (Dijckmann, 1927; Eaton, 1956; Grobman, 1959; Hilton, 1945, 1948, 1953; Lüdike, 1955; Martof and Rose, 1962; Piatt, 1935; Soler, 1950); physiology (Blair, 1961; Dent *et al.*, 1955; Dent and Kirby-Smith, 1963; Dent and Schuellein, 1950; Hutchison, 1961; Vernberg, 1955); water hygiene (Hassler, 1932); cytology and histology (Bernstein, 1953; Craig *et al.*, 1955; Enlow and Brown, 1956). Organ (1961a) reviewed all information pertaining to the eggs and newly hatched larvae. Discussions of the evolutionary relationships between *Gyrinophilus* and other plethodontid salamanders may be found in Dunn (1926), Noble (1927, 1931), and Piatt (1935).

The following species and subspecies of *Gyrinophilus* have been recognized generally.

FIG. 1. Adults of *Gyrinophilus porphyriticus:* A. Neotype of *G. p. porphyriticus*, Meadville, Crawford Co., Pa. (MCZ 35778); B. *G. p. duryi*, Laurel Cave, Carter Co., Ky. (RB 777); C. *G. p. dunni*, near Blue Ridge, Fannin Co., Ga. (RB 782); D. *G. p. danielsi*, Indian Gap, Great Smoky Mountains National Park (JEH).


A
B
C
D


A
B
C
D

Gyrinophilus porphyriticus porphyriticus (Green, 1827)
Gyrinophilus porphyriticus duryi (Weller, 1930)
Gyrinophilus porphyriticus inagnoscus Mittleman, 1942
Gyrinophilus danielsi danielsi (Blatchley, 1901)
Gyrinophilus danielsi dunni Mittleman and Jopson, 1941
Gyrinophilus danielsi polystictus Reese, 1950
Gyrinophilus lutescens (Rafinesque, 1832)
Gyrinophilus palleucus palleucus McCrady, 1954
Gyrinophilus palleucus necturoides Lazell and Brandon, 1962
Gyrinophilus palleucus gulolineatus Brandon, 1965

The designation *Gyrinophilus warneri* has appeared in two abstracts (Sinclair, 1953, 1955) without a description and was used for specimens discussed before the Tennessee Academy of Science. It is a *nomen nudum.* The specimens, made available to me by Sinclair, are not members of the genus *Gyrinophilus,* but of *Pseudotriton, sensu stricto.*

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FIG. 2. Adults of *Gyrinophilus porphyriticus:* A. Intergrade between *G. p. porphyriticus* and *G. p. duryi* showing the *inagnoscus* pattern, Hocking Co., Ohio (RB 774); B. New England pattern variant of *G. p. porphyriticus*, Stockbridge, Vt. (MCZ 37177); C. Cloudland Canyon, Dade Co., Ga. (RB 769); D. Near Lock 13, Tuscaloosa Co., Ala. (RB 835).

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I am indebted to Thomas C. Jegla for his instruction and assistance with the histological examinations, to M. J. Greenberg for the use of his laboratory facilities, to J. A. Waitz for suggestions in the statistical analyses, and to C. E. Pfluger for the use of the facilities of the x-ray laboratory in the University of Illinois Department of Chemistry.

Above all, I sincerely appreciate Dr. Hobart M. Smith's assistance and guidance throughout the course of this investigation.

MATERIALS AND METHODS

Living adult specimens were examined from the following areas:

Alabama: Talladega, Tuscaloosa, and Jackson counties.
Georgia: Dade, Fannin, Rabun, and Towns counties.
Kentucky: Carter and Lewis counties.
Maryland: Garrett County.
North Carolina: Cherokee, Macon, and Swain counties.
Ohio: Adams, Hamilton, Hocking, Pike, Scioto, and Washington counties.
Pennsylvania: Berks and Crawford counties.
Tennessee: Franklin, Grundy, Hamilton, McMinn, Roane, Sevier, and White counties.
Vermont: Windsor County.
Virginia: Grayson and Nelson counties.
West Virginia: Pocahontas County.

Detailed external examinations were made of approximately 1450 preserved specimens (950 adults, 500 larvae) obtained from the sources listed in the Acknowledgments. A few specimens are still in my personal collection (RB).

Accurate counts of trunk vertebrae were obtained from radiographs. Exposures were made from a distance of 19 inches on Ansco Industrial Superay 'B', extra fine grain, high contrast x-ray film at 20 KVP, 10 MA for 0.5 to 1.5 minutes, depending on specimen size, using an AEG 50 tungsten target tube. The radiographs were of sufficient detail to be useful in examination of certain cranial features.

In the analyses of geographic variation the following measurable characters were used:

Snout-vent length: measured ventrally (to nearest mm) from snout tip to anterior border of cloaca with an mm (scale). Unless stated otherwise, all length notations are snout-vent measurements.

The next three characters were measured with an ocular micrometer in a binocular dissecting microscope.

Diameter of choana: measured (to nearest 0.1 mm, estimated to nearest 0.01 mm) at right angles to long axis of head at a magnification of 27 ×.

Internal head width: distance (to nearest 0.1 mm) between hindmost teeth of the maxillary bones under 18 × or 27 × magnification.

Upper jaw length: distance (to nearest 0.1 mm) from medial suture between premaxillary bones to hindmost tooth on maxilla (average of both sides) at 18 × magnification.

Costal grooves: the number of grooves between anterior and posterior limbs, counting one in the axilla and one in the groin (usually); forking grooves in groin counted as two.

Premaxillary and maxillary teeth: counted in strong illumination under magnification of 27 ×; counts from both bones of both sides combined.

Prevomerine and paravomerine teeth: counted jointly as in preceding.

Continual tooth replacement, and the loss of teeth after preservation, may introduce erroneous tooth counts. An attempt was made to count tooth sockets and reduce at least part of the error involved.

Sex determination of adult specimens was based on the configuration of the cloacal walls, simply folded in females and with many small papillae on the anterior half in all males (Bishop, 1941). Although these papillae are most pronounced during the breeding season, they are always revealed by careful examination. No other secondary sex characteristic was apparent.

A few adult and larval specimens were cleared and stained by the KOH-Alizarin Red S method (Williams, 1941). Histological examinations were made of serial sections of adult and larval heads fixed in AFA (alcohol-formalin-acetic acid), decalcified in picric acid (saturated aqueous solution) for several days, dehydrated in ethyl alcohol, cleared in xylene, imbedded in paraffin, cut at 10–12 micra and stained with Mallory's triple connective tissue stain.

Sample means of data presented in several figures are compared by Duncan's Multiple Range Test (DMRT) (Duncan, 1955).

Only the first reference to a combination is cited in notations of synonymies of the forms included in the genus *Gyrinophilus.*

GENUS *GYRINOPHILUS* COPE

Gyrinophilus Cope, 1869:108–109 (type-species *Salamandra porphyritica* Green, 1827, by monotypy).
[*Pseudotriton*]: Grobman, 1959:60–63 (in part).

Diagnosis of Fully Metamorphosed Individuals. Plethodontid salamanders with the following combination of characteristics (Fig. 3C, E): tongue free all around; premaxillae usually separate (fused 2 per cent of specimens); a fontanel between unfused nasal processes of premaxilla; septomaxilla present; prefrontals present, not reaching nares in adults; prevomerine and paravomerine teeth continuous; occipital condyles not stalked; canthus rostralis present.

Diagnosis of Branchiate Individuals. Larval plethodontid form (no ypsiloid cartilage, anterior projection of pubis, or lungs); 3 epibranchials; tail fin not extending onto body as dorsal body fin; 18–20 trunk vertebrae (17–19 costal grooves between limbs); premaxilla single, nasal processes unfused and well separated (Fig. 3B).

Range. Appalachian uplift of eastern United States and adjacent Canada as far north as western Maine and southern Quebec, extending into adjacent areas to the west from Cincinnati, Ohio, to northeastern Mississippi, and the Fall Line in Alabama.

Remarks. Cope (1869) characterized the genus *Gyrinophilus* as distinct from *Spelerpes* (*Eurycea* and *Pseudotriton*) by the following characteristics: (1) ". . . the premaxillary bones remaining distinct, and embracing a fontanelle"; (2) "Its nasal bones are well separated . . ."; (3) "The anterior or prootic crest is short, distinct and curved inwards and backwards; that on the proximal extremity of the squamosal curves towards it, but leaves a considerable interspace." "In S. *ruber* the anterior crest only is present. . . ." In Dunn's treatment of the family Plethodontidae (1926), the only cranial features used to separate *Pseu-*

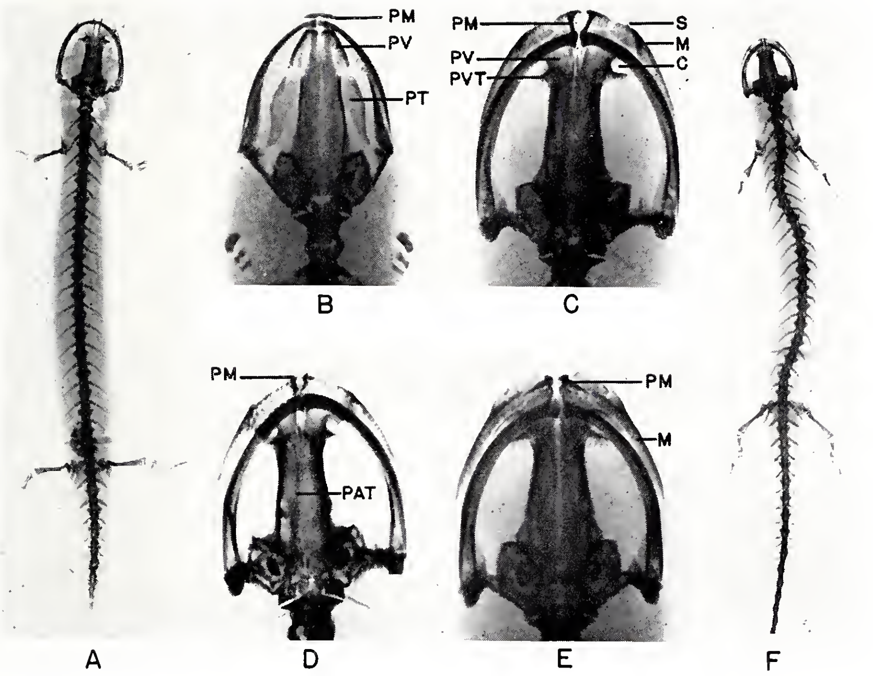

FIG. 3. Radiographs of adult *Gyrinophilus porphyriticus* (A, C, E), adult *Pseudotriton ruber* (D, F), and larval *Gyrinophilus* (B). Abbreviations used are: PM (premaxilla), PV (prevomer), PVT (prevomerine teeth), M (maxilla), C (choana), S (septomaxilla), PAT (paravomerine teeth), PT (pterygoid bone).

dotriton from *Gyrinophilus* were the presence of two premaxillae, and nasals not bordering the nares in the latter.

Grobman (1959) presented studies of the bones used in the diagnosis of the genus and critically reviewed the characteristics of the genus as outlined by Cope (1869) and Dunn (1926). Grobman felt that the features previously employed as generic characters are subject to sufficient ontogenetic change and overlap with those of *Pseudotriton* that they will not identify both larvae and adults, and that they are therefore not sufficient to distinguish *Gyrinophilus* from *Pseudotriton*. He therefore recommended the inclusion of members of *Gyrinophilus* in the genus *Pseudotriton*.

Martof and Rose (1962), re-evaluating information on the cranial morphology of *Gyrinophilus* and *Pseudotriton*, concluded that the two genera can be distinguished by the following criteria: compactness of cranial construction, density and relative length of cranial bones, the ontogeny and shape of nasals and their contact with the maxillae, and the condition of the premaxilla. The present studies necessitate the further review of the data presented by Grobman and Martof and Rose relative to an evaluation of the relationship between *Gyrinophilus* and *Pseudotriton.*

Anterior rami of premaxilla. Grobman found that the anterior rami are usually separate in fully metamorphosed *Gyrinophilus* and that they are fused in comparable specimens of *Pseudotriton.* However, since the rami are fused in larvae of both *Gyrinophilus* and *Pseudotriton,* he considers this to be a poor character, even though it suffices to separate most adult specimens (see below for exceptions). Of 260 specimens of *Gyrinophilus* examined by me using radiographs (Fig. 3), 40 had anterior rami incompletely separated. The body size and dentition of 20 of these specimens indicate that they were in terminal phases of metamorphosis, or had recently metamorphosed; the remaining 20 were definitely post-metamorphic. Since larval *Eurycea, Pseudotriton,* and *Typhlotriton,* in addition to *Gyrinophilus,* have fused anterior rami (Martof and Rose, 1962; personal observation), it is not surprising that this condition persists in newly metamorphosed *Gyrinophilus,* although complete separation of the rami will normally accompany final, full metamorphosis. Of the 20 post-metamorphic specimens, only 6 had anterior rami completely fused as in *Pseudotriton.* In the remaining 14, fusion of the rami varied. In some only a tiny bridge of bone connected the two rami; in others the point of fusion was conspicuously marked by a narrowing of the bone. Cases of incomplete separation were readily distinguished from the fused *Pseudotriton* condition. Of the 260 specimens, only 2.3 per cent could have been incorrectly identified as *Pseudotriton* on the basis of the fused anterior rami of the premaxilla. Even these are correctly identified by the separate nasal processes and by other cranial traits.

Nasal process of premaxilla. Grobman noted that larval and adult *Gyrinophilus* have separate nasal processes, whereas in the adult and larger larval *Pseudotriton* these processes are fused. The separate nasal processes will separate all adult *Gyrinophilus* from all adult *Pseudotriton.* This accords with my data.

Nasals. Grobman concluded that, because of variation and/or ontogenetic change, differences in the nasals are not dependable generic traits, and therefore are not of diagnostic value. Martof and Rose, however, found certain aspects of the ontogeny and the shape of the nasals to be diagnostic. In *Pseudotriton,* the nasals ossify in large larvae, and in adults they are separated from the maxilla by prefrontals which reach to the nares. No larval specimen of *Gyrinophilus* examined by Martof and Rose had nasal bones; these elements appeared at or slightly after transformation. In adults they are in broad contact with the maxillae (see also Figure 1 in Martof and Rose, 1962).

These cranial features do distinguish fully metamorphosed specimens of *Gyrinophilus* from *Pseudotriton* (anterior rami and nasal processes of premaxilla, nasals, prefrontals, bone density, and compactness of construction), and there are at least two features distinguishing larger larvae (nasal processes of premaxilla, and nasal bones). The presence of neotenic species in some genera of plethodontid salamanders (e.g., *Eurycea* and *Gyrinophilus*) demonstrates a need for more inclusive generic diagnoses to include branchiate specimens. Most generic diagnoses have been based solely on the characteristics of adults, and little or no consideration has been given the larvae with their generally more similar structure. The neotenic species *Gyrinophilus palleucus* does not fit Cope's diagnosis of the genus, but it is similar to the larvae of *G. porphyriticus* in most cranial and body features.

The degree of structural difference between adult and larval *Gyrinophilus* and *Pseudotriton* is of the same magnitude as that between other genera of plethodontid salamanders. The distinctions noted here are dependable indicators within generally acceptable limits. They are correlated with even more significant differences in life history and ecological niche (see Martof and Rose, 1962), and demonstrate that the taxonomic distinction of the two genera conforms with the commonplace concept of the role of the genus.

Summary. Although comparison of the ontogenetic development of the several cranial elements examined by Grobman is interesting from the standpoint of phylogenetic interpretation, it is not sufficient to invalidate the generic status of *Gyrinophilus.*

Referred forms.

Gyrinophilus porphyriticus porphyriticus (Green), 1827:3.
Gyrinophilus porphyriticus duryi (Weller), 1930:6–9.
Gyrinophilus porphyriticus danielsi (Blatchley), 1901:760–762.
Gyrinophilus porphyriticus dunni Mittleman and Jopson, 1941:1–5, pl. 1 (in part).
Gyrinophilus palleucus palleucus McCrady, 1954:200–206.
Gyrinophilus palleucus necturoides Lazell and Brandon, 1962:300–306.
Gyrinophilus palleucus gulolineatus Brandon, 1965:346–352.

KEY TO SPECIES AND SUBSPECIES OF *Gyrinophilus*

1. Form larval; external gills present 2
   Metamorphosed; no external gills .... *porphyriticus* 5
2. Diameter of eye entering distance from anterior corner of eye to snout tip 4–5 times .... *palleucus*.............. 3
   Diameter of eye entering distance from anterior corner of eye to snout tip 1.5–3.5 times .... *porphyriticus* larvae
3. Slightly pigmented dorsally; pale appearance .... *p. palleucus*

Uniformly dark brownish-purple dorsum; large specimens with large dark dorsal spots 4

4. Nineteen–twenty trunk vertebrae; no dark stripe or blotch on anterior part of throat . . . . *p. necturoides*

Eighteen–nineteen trunk vertebrae; a dark stripe or blotch on anterior part of throat . . . . *p. gulolineatus*

5. Dark dorsal pigment mottled or reticulated, without spots dorsally . . . . *p. porphyriticus*

Dorsum not mottled or reticulated, but clear with superimposed tiny to moderately large black dots and flecks 6

6. Dorsum profusely flecked with black . . . . *p. dunni*

Dorsum with scattered black dots and flecks, but not profusely flecked 7

7. Canthus rostralis distinct, bordered by black; paravomerine tooth series not convergent anteriorly . . . . *p. danielsi*

Canthus rostralis indistinct, not bordered by black; paravomerine tooth series conspicuously convergent anteriorly; dorsal dots and flecks usually concentrated dorsolaterally . . . . *p. duryi*

GEOGRAPHIC VARIATION

Number of Trunk Vertebrae

Accurate counts of trunk vertebrae (hereafter referred to simply as vertebrae) were obtained from radiographs of 662 specimens of *Gyrinophilus porphyriticus* and *G. palleucus* selected from representative areas throughout their ranges. In *Gyrinophilus* the number of vertebrae ranges from 17 to 20. Of 662 specimens, 42 per cent had 18, 50 per cent, 19, 2 per cent, 20, and one specimen, 17 vertebrae. No count is unique for any particular geographic area. Specimens with 18 and 19 vertebrae were found throughout the range of the genus. Specimens with 20 vertebrae were found in populations having predominantly 19. The one specimen with 17 vertebrae was collected at Lookout Mountain, Dade Co., Ga., in a population usually having 18 vertebrae.

There is a change in relative frequencies of 18 and 19 vertebrae in different geographical regions (Fig. 4).

More than 79 per cent of all individuals examined from the following geographical regions had 19 vertebrae: (1) New England and Canada, (2) eastern and southeastern Ohio, and (3) most parts of Tennessee, Georgia, and Alabama. More than 79 per cent of the sample from most parts of New York and Pennsylvania and northwestern South Carolina

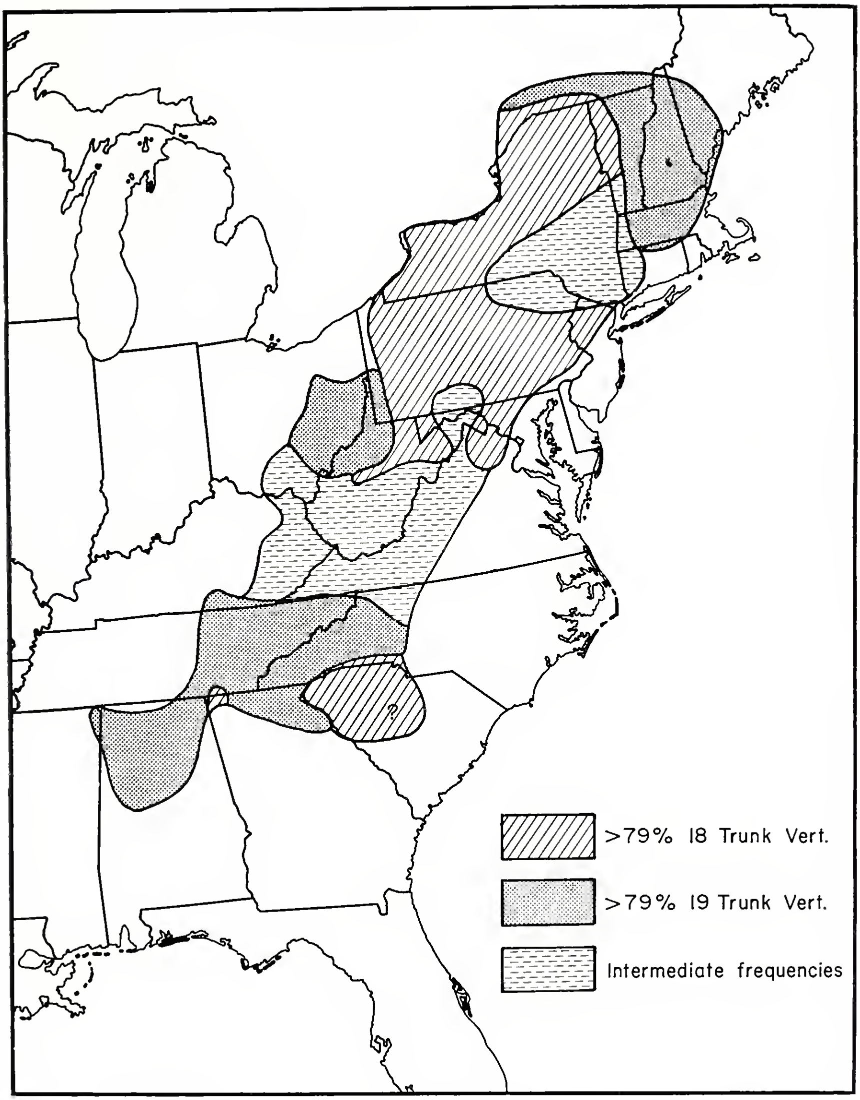

Fig. 4. Geographic variation of relative frequencies of trunk vertebral number in *Gyrinophilus porphyriticus*.

had 18 vertebrae. Areas of intermediate relative frequencies are (1) eastern New York and northeastern Pennsylvania, (2) the area throughout southern Ohio, eastern Kentucky, southern West Virginia, and adjacent Virginia.

The percentage of 18 trunk vertebrae in samples of each subspecies was as follows (differences from 100 per cent represent percentages with 19–20 vertebrae): *G. p. porphyriticus* (64); *G. p. duryi* (47); *G. p. danielsi* (17); *G. p. dunni* (25); *G. palleucus palleucus* (52); *G. palleucus necturoides* (0); *G. palleucus gulolineatus* (80).

It is difficult to assign any significance to the distributional pattern of vertebral variation with present data. It is possible, as has been shown to be the case in fish (Barlow, 1961, and references therein), that variation in vertebral number may result in part from environmental effects on the genotypic range of expression. Highton (1957) observed that over 80 per cent of individuals of many species and subspecies of *Plethodon* have the same vertebral number. To determine the significance of these observations he (1960) collected a large series of *Plethodon cinereus* egg clusters with their attendant females, compared vertebral numbers of the females and their offspring, and calculated estimates of heritability for vertebral number of 0.57 and 0.61 based on the use of correlation coefficients and on the regression coefficient method respectively. The eggs of *Gyrinophilus* have been found in nature only three times (Organ, 1961a). Experiments similar to Highton's, using *Gyrinophilus* as subjects, may never be feasible because of collecting difficulties.

A detailed treatment of the genus *Plethodon* (Highton, 1962) points out taxonomic implications of geographic variation in number of vertebrae. Among 16 species of *Plethodon* the modal number ranges from 14 to 23. In two of the five species in which subspecies were recognized, the difference in modal number of vertebrae is diagnostic at the subspecies level. Reports of variation with the geographic distribution of other genera of salamanders are few, although such variation predictably may occur in most. Rabb (1958) reported that, in six taxa of the Central American genus *Chiropterotriton*, variation was so slight that it was of no taxonomic use. Tihen (1958), in his study of the family Ambystomatidae, noted that the number of vertebrae was constant within narrow limits of variation for a given species, but presented no data on relative frequencies or geographic variation.

The variability of vertebrae in *Gyrinophilus* prevents their being used in identifying to species and subspecies. Highton's work with *Plethodon* may well indicate that this character may become useful in considerations of evolutionary and zoogeographical problems in *Gyrinophilus*.

In a report of studies on *Necturus*, Hecht (1958) concluded after x-ray examination of the vertebral columns of an unlisted number of specimens that "the costal groove count was a good indicator of the position of the pelvic girdle and the number of vertebrae which were between the two girdles. The number of costal grooves showed limited geographic variability and were not too useful in identification." Other recent papers dealing with the systematics of certain groups of salamanders (e.g., Hendrickson, 1954) mention differences in the number of costal grooves in different taxa, but give no indication of the relative frequencies or geographic distribution of variants.

Radiographs of trunk vertebrae of *Gyrinophilus* revealed similarities to those of *Plethodon* (Highton, 1957) in the relationship between costal grooves and trunk vertebrae, between the girdles and vertebrae, and of some skeletal anomalies. Such factors must be taken into account in determining the number of trunk vertebrae accurately.

As in *Plethodon* and other genera examined by Highton, when bifurcate grooves in the groin are counted as two, the number of costal grooves is usually one less than the number of trunk vertebrae. The first costal groove varies in position with shifts in the position of the pectoral girdle relative to the vertebrae. However, it is dorsal to, in, or immediately posterior to the axilla. The pectoral girdle is opposite either the second trunk vertebra (6 per cent of a sample of 260 specimens), the joint between the second and third trunk vertebrae (72 per cent), or the third trunk vertebra (22 per cent).

Highton noted that in *Plethodon* the last trunk vertebra was ribless. Although ribs on the hindmost one or two trunk vertebrae were usually reduced in size, the last presacral vertebra actually lacked ribs in only 3.8 per cent of 662 specimens of *Gyrinophilus*.

Two specimens of 662 examined had well-developed cervical ribs (MCZ 4274; NMC 2118), but, except for these, the cervical vertebrae appeared to be similar to those of other specimens.

The position of the pelvic girdle varied considerably, and, as in *Plethodon* (Highton, 1962), this accounted for most of the error in estimating the number of trunk vertebrae from counts of costal grooves. The position was either (a) between the sacral and last presacral vertebra (3 per cent of 260 specimens), (b) opposite the sacral (15 per cent), (c) between the sacral and first caudal (56 per cent), (d) opposite the first caudal (25 per cent), or (e) between the first and second caudals (only one specimen). In two specimens, the ilium articulated with the sacral on the right side and the last presacral on the left. A count of costal grooves would result in an inaccurate estimate of the number of trunk vertebrae when items (a), (e), and some (d) are operative. The frequency of inaccurate estimates could thus be as high as 29 per cent (although some of the specimens (d) would be correctly estimated). Thus in *Gyrinophilus* the dependability of estimates based on costal groove counts is much lower than in *Plethodon*, where Highton found a probable error of estimate of only 6 per cent.

Eight instances of fused vertebrae in a sample of 850 specimens were noted. No particular vertebrae seemed more prone to fuse than others. In all cases the ribs were normal in number. These were all associated with costal grooves and had no effect on estimates of trunk vertebrae. To obtain a count of trunk vertebrae comparable with those of other specimens from the same geographical area, each member of a set of fused vertebrae had to be counted individually.

UMMZ 122746	12th–13th vert.	2 ribs on each side
UIMNH 50481	1st–2nd vert.	2 ribs on each side
UIMNH 50436	4th–5th vert.	2 ribs on each side
CU 4086	1st–2nd vert.	2 ribs on each side
CNHM 36613	19th–20th vert.	2 ribs on each side
BDV	16th–17th vert.	2 ribs on right side, 1 on left
WVBS	3rd–4th vert.	2 ribs on left side, 1 on right
UIMNH 50137	9th–10th–11th vert.	3 ribs on each side
UIMNH 50137	13th–14th–15th vert.	3 ribs on each side
NMC 5074	9th–10th–11th vert.	3 ribs on each side

VENTRAL PIGMENTATION

The presence and distribution of melanophores on the throat, pectoral region, and belly have been used as characters for the identification of several subspecies of *G. porphyriticus;* e.g., *polystictus, danielsi,* and *dunni* (Reese, 1950; Blatchley, 1901; Bishop, 1943; Mittleman and Jopson, 1941), and have received cursory mention in discussions of *duryi, inagnoscus,* and *porphyriticus* (Dunn, 1926; Bishop, 1941; Mittleman, 1942). Little attempt has been made, however, to clarify the ontogenetic development or geographical variation of this feature within these taxa and the genus as a whole.

The presence of black reticulations on the throat was used by Blatchley (1901) as a distinctive feature of *danielsi.* Bishop (1943, p. 364), in his discussion of this form, noted that "The entire throat and, in some old individuals, the region back of the gular fold, as well as the lower edge of the upper lip, may be finely reticulated with black and white in about equal proportions. In younger individuals these reticulations may be almost lacking." This statement is the earliest recognition that ontogenetic changes in pigmentation occur in *danielsi.* Reese (1950, p. 2) partly characterized *polystictus* by "the throat heavily reticulated to the insertion of the forelimbs, and venter sparsely dotted. . . ." He distinguished *polystictus* from *danielsi,* noting that "in *G. danielsi danielsi* the dorsal spots are smaller and sparser, the venter is immaculate, and the throat reticulations rarely reach the gular fold." Data presented in the systematic treatment of *G. p. danielsi* show that the pigmentary characters of populations described by Reese as *polystictus* actually do not differ from those of *danielsi,* and that insufficient material was available to him.

Mittleman and Jopson (1941, p. 2) discussed pigmentation in *dunni,* and noted that "There are often a few very tiny spots or flects widely distributed on the venter, but in no case is the ventral surface so heavily suffused with markings as it is in *danielsi;* indeed, it is generally immaculate."

In *porphyriticus, inagnoscus,* and *duryi* ventral pigmentation has not aroused as much interest, and it has been used but little in their differential identification. Dunn (1926, pp. 261–262) mentioned "dots of black on the belly and a good many on the throat and the edge of the lower lip . . ." of MCZ 5628, from Midway, Nelson Co., Va., but he treated this condition as merely a variation from the unpigmented condition. Bishop (1941, p. 240) recognized ontogenetic changes in belly pigment in New York specimens, noting "In very old specimens the entire back may become very dark and pigment appears in flecks and small spots on the throat and belly, and in a dark band on the lower lip." Mittleman (1942, p. 27) noted that *inagnoscus* differed from *porphyriticus* in that the "ventral stippling [is] finer and more sparsely distributed. . . ." Mittleman applied the name *inagnoscus* to intergrade populations between *G. p. porphyriticus* and *G. p. duryi* (see the section herein dealing with *G. p. porphyriticus*).

Ventral pigmentation of *duryi* was well characterized by Bishop (1943, p. 372): "The ventral surfaces, with the exception of the lower lip and occasionally the throat and gular region, are free from the dark spots."

Since it appears from other evidences (trunk vertebrae, tooth characters, distribution, and intergradation among described forms) that the epigean populations of *Gyrinophilus* are all subspecies of the widely distributed species *porphyriticus,* more precise information bearing on the geographic variation of ventral pigmentation would be useful in forming a clearer understanding of the distribution of the several forms, and of the relationships among them. Data for Fig. 6 were collected from 312 specimens of *G. p. porphyriticus* (including *inagnoscus*) and *G. p. duryi* over 79 mm in length. A subjective estimate of the amount of dark pigment on the belly of each specimen was made. A length of 79 mm was used for two reasons as a reference point: (1) the mean snout-vent length of the completely metamorphosed specimens studied was near 80 mm, and (2) data in Fig. 5 suggest that ventral pigmentation with few exceptions, does not develop immediately after metamorphosis. Rather it develops gradually with increase in length. The specimens most heavily pigmented ventrally were generally the longest ones. Presumably, they are also the oldest, but the correlation between size and age is only approximate, since in amphibians growth is greatly modified by ambient temperature and food intake. Specimens with pigmented ven-

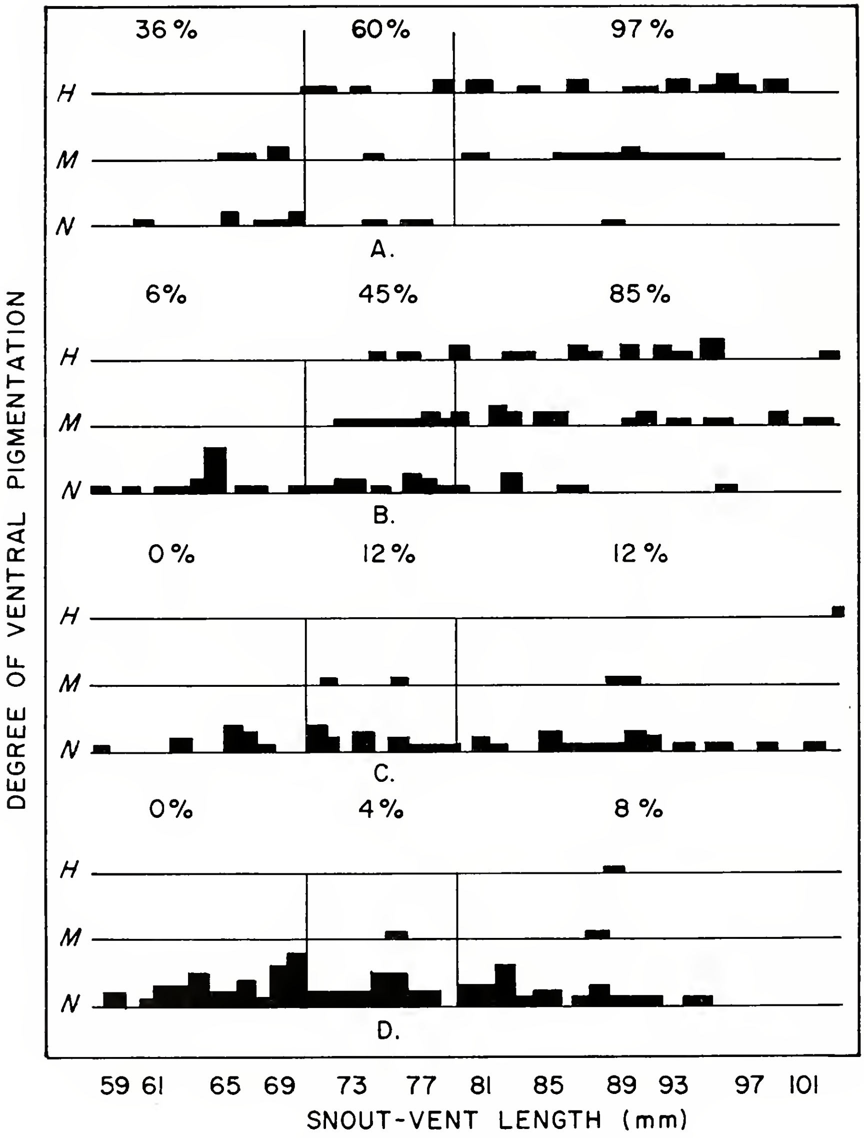

FIG. 5. Ontogenetic development of ventral pigment in *G. porphyriticus*: A. Central New York; B. Pennsylvania and northern West Virginia; C. Ohio, other than *p. duryi*; D. Ohio, Kentucky, and West Virginia *p. duryi*. Degrees of pigmentation are (H) heavily, (M) moderately, and (N) not pigmented. Percentages of moderately and heavily pigmented specimens in each size class are indicated.

ters and those with unpigmented venters were found together throughout most of the combined ranges of *p. duryi* and *p. porphyriticus*. Geographically, the relative frequencies of the two conditions vary considerably (Fig. 6). In all samples from the northeastern states, except Maine, over 80 per cent of specimens had moderately to heavily pigmented bellies, with the highest percentage in central New York. At the other extreme, fewer than 5 per cent of the specimens collected in southeastern and northern Kentucky were moderately to heavily pigmented. Intermediates were obtained from West Virginia south to Alabama.

G. porphyriticus appears typically to become progressively more heavily pigmented ventrally with the increase in length after metamorphosis; *duryi* and *dunni* typically possess melanophores only along jaw borders; the intensity of ventral pigmentation in *danielsi* (see also the section dealing with this form) varies ontogenetically and with elevation. Specimens collected at high elevations are characterized by throats heavily reticulated with black, whereas venters of specimens from low elevations are without melanophores. In areas which are otherwise shown to be zones of intergradation between *p. porphyriticus* and *p. duryi*, there is an intermediate frequency of heavily dotted venters.

New England populations of *p. porphyriticus* seem to be slightly different from most *p. porphyriticus* in ventral pigmentation, as well as in number of vertebrae, but the pigmentary difference may be due to secondarily bleached specimens. Most of the large, clear-bellied New England specimens were in the same collection. Specimens in other collections from the same locality had heavily pigmented bellies.

In summary, there is some correlation between ventral pigmentation and subspecies in *G. porphyriticus*, but the correlation is not precise, possibly because of post-Pleistocene genetic mixing (see section herein dealing with zoogeographic considerations) and bleaching of specimens after collection.

Ventral pigmentation was used in identifying only one subspecies, *G. palleucus gulolineatus*. The venter on all specimens of *p. palleucus* and *p. necturoides* examined was without pigment. The largest specimens of *p. gulolineatus*, on the other hand, in addition to the characteristic dark throat stripe, have dark flecks and dots scattered over the pectoral region and belly.

Tooth Characters

SHAPE OF PREVOMERINE AND PARAVOMERINE SERIES

Mittleman (1942) used the shapes of the prevomerine (vomerine of some authors) and paravomerine (parasphenoid) tooth series as diagnostic features of several subspecies of *G. porphyriticus*. His figures of

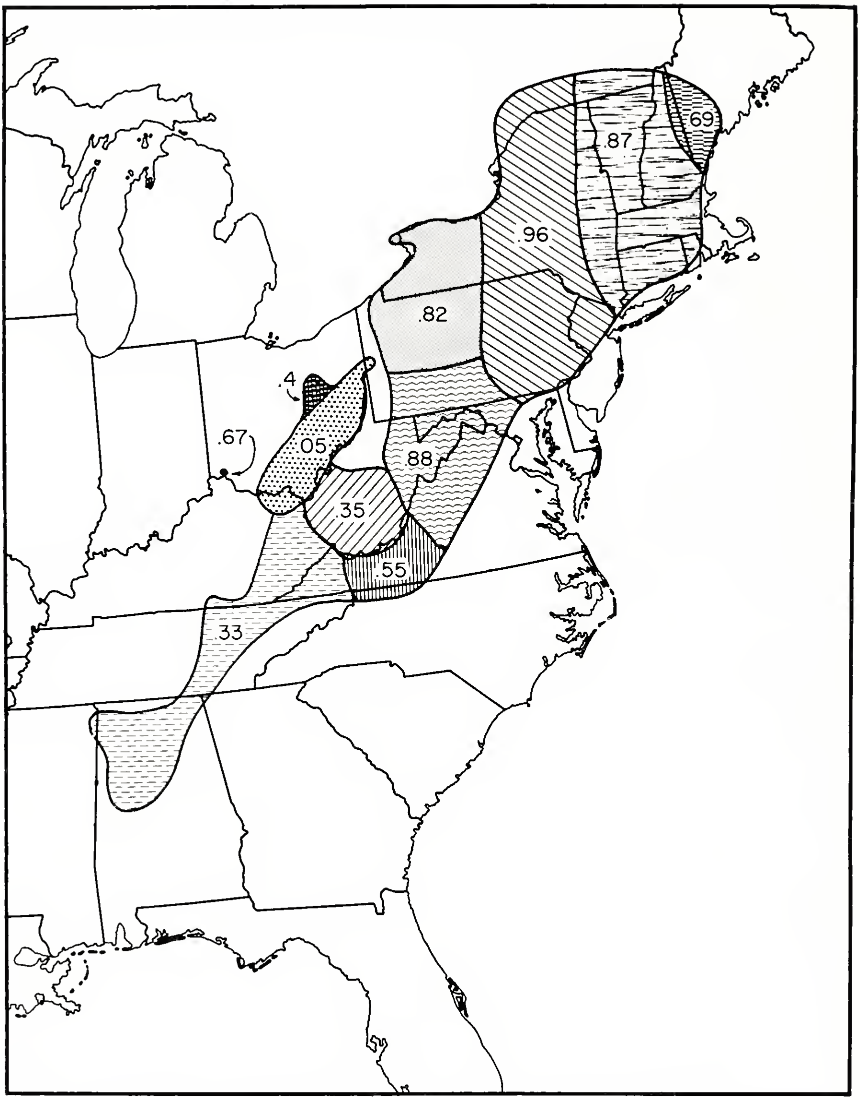

FIG. 6. Geographic variation in ventral pigmentation in *G. p. porphyriticus* and *G. p. duryi* (intergrades between *p. porphyriticus* and other subspecies included): Numbers indicate frequency of sample with moderately to heavily pigmented bellies. All specimens are over 79-mm snout-vent length.

these series (Figs. 1–5), however, are not characteristic of the forms represented. Although certain tooth series features are characteristic of certain subspecies, considerable variation was found, even among individuals from the same locality. It was necessary to investigate the amount and significance of variation encountered within and among subspecies.

G. p. porphyriticus (Fig. 8A, B, C):

Material examined: NEW YORK: *Albany Co.* (CNHM 91155, 91159, 91160). *Broome Co.* (CU 4086, 5615). *Cattaraugus Co.* (CNHM 91164, 91177, 91183, 91185–6, 91189, 91200–1, 91203, 91205). MAINE: *Oxford Co.* (UMMZ 122746).

To facilitate discussion, the terms transverse and longitudinal will be used instead of prevomerine and paravomerine tooth series. As Bishop (1943, pp. 368, 371, 374) pointed out, the prevomerine series includes the transverse and part of the longitudinal series as well. The anterior end of the longitudinal series, the angle between it and the transverse, and the transverse series itself all lie on the prevomerine bone (Fig. 7). Most of the longitudinal series lies on the parasphenoid bone, but the teeth are actually borne on posterior extensions of the prevomer (as shown in *Eurycea bislineata* by Wilder, 1925). For this reason Taylor (1944, p. 206) called these teeth paravomerine instead of parasphenoid, and I follow his usage.

The most frequent configuration observed in *p. porphyriticus* was similar to that in Mittleman's Fig. 3 (1942, p. 31). The longitudinal series were close together anteriorly, but they gradually diverged posteriorly. Usually the transverse extended laterally at a right angle to the longitudinal series, but sometimes they formed less than a right angle, especially in recently metamorphosed individuals (Fig. 8B). The angle of the junction of the two series was usually sharp, but sometimes it was broadly rounded. The transverse series usually formed a straight line; occasionally this was a broadly curving line.

G. p. duryi (Fig. 8D, E):

Material examined: KENTUCKY: *Carter Co.* (OUVC 2686, 2688, 3012, 3919; RB 777). OHIO: *Pike Co.* (OUVC 3256, 3438–9, 3673, 3946). *Scioto Co.* (OUVC 3085). WEST VIRGINIA: *Cabell Co.* (WVBS 1296, 1746, 2299, 2401).

In all specimens examined by me the longitudinal series were close together anteriorly and divergent posteriorly. In some cases, however, the two rows of this series were more widely separated anteriorly than on any specimen of *p. porphyriticus* examined (Fig. 8D). The union of the transverse and longitudinal series varied from a right angle to acute and obtuse configurations, varying from sharply angular to broadly curved arcs. The transverse series sometimes formed a straight line, a broadly curved line, or, occasionally, a recurved line (Fig. 8E). The most characteristic feature of the two tooth series of this subspecies was the variation they exhibited.

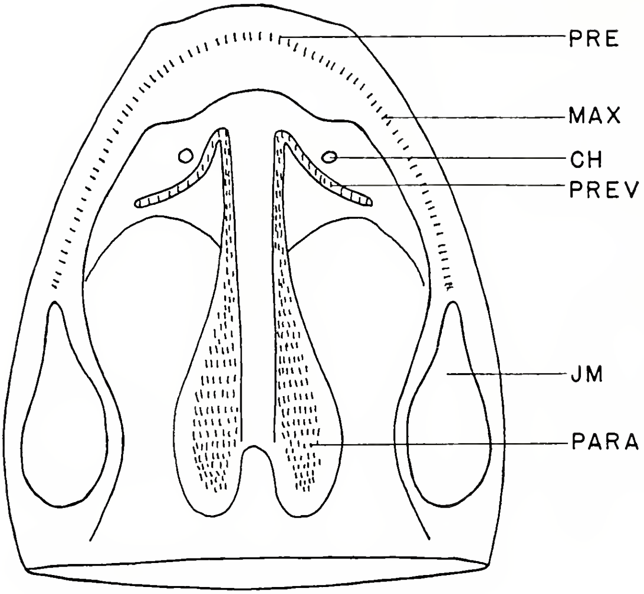

FIG. 7. Sketch showing position of tooth series in roof of metamorphosed *Gyrinophilus* mouth. Abbreviations used are: PRE (premaxillary teeth), MAX (maxillary teeth), CH (choana), PREV (prevomerine teeth), JM (jaw musculature), PARA (paravomerine teeth).

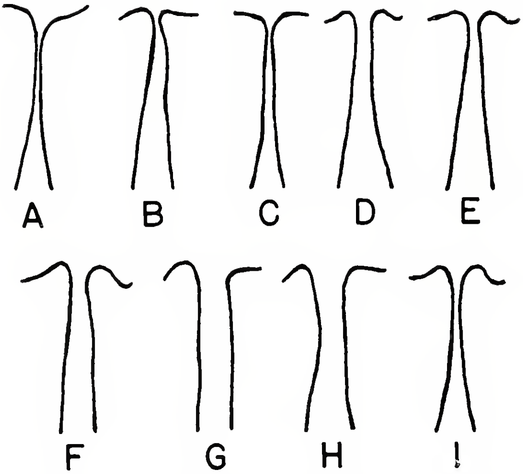

FIG. 8. Shapes of pre- and paravomerine tooth series in *G. p. porphyriticus* (A, B, C), *G. p. duryi* (D, E), *G. p. dunni* (F), *G. p. danielsi* (G, H), Alabama specimens (I).

G. p. inagnoscus (Fig. 8A-E):

Material examined: OHIO: *Athens Co.* (OUVC 2966). *Hocking Co.* (OUVC 3175, 3871, 3896; RB 774).

The shapes of the transverse and longitudinal tooth series fell within the variation seen in *p. porphyriticus* and *p. duryi.*

G. p. dunni (Fig. 8F):

Material examined: GEORGIA: *Clarke Co.* (UG 552). *Fannin Co.* (RB 779, 782). *Rabun Co.* (CM 17792; OUVC 3969–70). *Towns Co.* (UG 568, 969, 1220). NORTH CAROLINA: *Cherokee Co.* (HCY). *Macon Co.* (UG 931). SOUTH CAROLINA: *Oconee Co.* (UG 933; USNM 113230). TENNESSEE: *Monroe Co.* (UIMNH 50148).

The shape formed by the two tooth series is quite different in several ways from that of *p. porphyriticus* and *p. duryi.* The longitudinal series were usually widely separated for their full length, but slightly convergent anteriorly. The transverse series, except on newly metamorphosed individuals, was recurved, and joined the longitudinal series in a rounded arc. Again, acute angles seemed to be characteristic of newly metamorphosed specimens, and probably represent a stage in the development of the adult condition. No specimen of *dunni* examined had a longitudinal series shaped like that shown by Mittleman (1942, Fig. 5, p. 36).

G. p. danielsi (Fig. 8G, H):

Material examined: Specimens from the Great Smoky Mountains National Park Collection (GDD 3–4, 7, 11–12, 14–15, 17–20; GdXd 1–2). All specimens were collected in the park, at various elevations. No attempt was made to correlate differences with elevation, because so little variation could be observed in the sample.

The longitudinal series were usually parallel but showed anterior convergence in 2 of the 13 specimens with one of these resembling that of Mittleman's Fig. 4 (1942, p. 36), except for a longer transverse series. On two other specimens the longitudinal series converged slightly midway along their length, diverging both anteriorly and posteriorly from this.

Alabama material (Fig. 8I):

Material examined: *Blount Co.* (GRT 218). *Jackson Co.* (BDV). *Lawrence Co.* (BDV). *Tuscaloosa Co.* (TU 4948; BDV).

These specimens all had the recurved transverse series noted in *p. dunni* and an anteriorly convergent longitudinal series like that in *p. porphyriticus* and *p. duryi.*

Remarks: Although the considerable variation in the alignment of the transverse and longitudinal tooth series makes them of little value in identifying individual specimens, certain shapes characterize three of the four subspecies of *G. porphyriticus,* and a trend can be followed from one subspecies to another. Extreme anterior convergence of the longitudinal series is characteristic of *p. porphyriticus, p. duryi,* and intergrades between them (called *p. inagnoscus* by Mittleman, 1942), slight convergence of *p. dunni* and some *p. duryi,* and none of most *p. danielsi.* In *p. dunni* the two series usually join in a broad arc, in *p. porphyriticus* in a sharp angle; other subspecies show variation between these two extremes. The transverse series in *p. porphyriticus* is usually a straight line, in *p. dunni* a recurved line. Recurved transverse series were seen in nearly half of the *p. duryi* and *p. danielsi.*

G. p. danielsi, the most distinct subspecies as judged by the other criteria given herein, also has the most distinctively shaped tooth series. *G. p. dunni* tooth series are next most distinctive, but more nearly resemble those of *G. p. porphyriticus.* Alabama populations, by this and by pigmentation criteria, are apparently intergrades among *p. porphyriticus, p. duryi,* and *p. dunni.* Thus, despite some correlation between tooth series shapes and certain taxa, individual variation renders this of little use for identifying individual specimens.

NUMBER OF PREVOMERINE AND PARAVOMERINE TEETH

On some radiographs a faint suture separates the prevomerine and parasphenoid bones, but the position of the suture could not be determined from external examination, and no distinction could otherwise be made between the teeth of the two series. Mittleman and Jopson (1941) did not detail how they counted prevomerine (vomerine) teeth on their uncleared and unstained specimens. Possibly they considered only teeth in the transverse series to be on the prevomerine bone. Even this would not permit accurate counts on the broadly curving prevomerine series. To avoid subjective distinction between teeth of the two series, all teeth of both series were counted jointly in the present study and all available specimens over 60-mm snout-vent length from which counts could be made were used.

Preliminary plots of tooth counts for population samples showed slight or no correlation with snout-vent length and variation within the most frequent size class usually encompassed the variation of the entire sample. Thus the highest counts were not taken from the longest specimens. The characteristic lack of sexual dimorphism in *Gyrinophilus* is also indicated by similarity of tooth counts in males and females.

In Fig. 9 are plots of the results of counts of prevomerine and paravomerine teeth on specimens collected from the different areas. The specimens represented on Fig. 9 include *p. duryi*—Carter Co., Ky., and Adams Co., Ohio; *p. porphyriticus* X *p. duryi*—Cincinnati, Ohio, Grayson Co., Va., and Hocking Co., Ohio; *p. porphyriticus*—Pennsylvania, New York, and New England; *p. danielsi*—Burke Co., N.C. Specimens of *p. duryi* in general have more prevomerine and paravomerine teeth

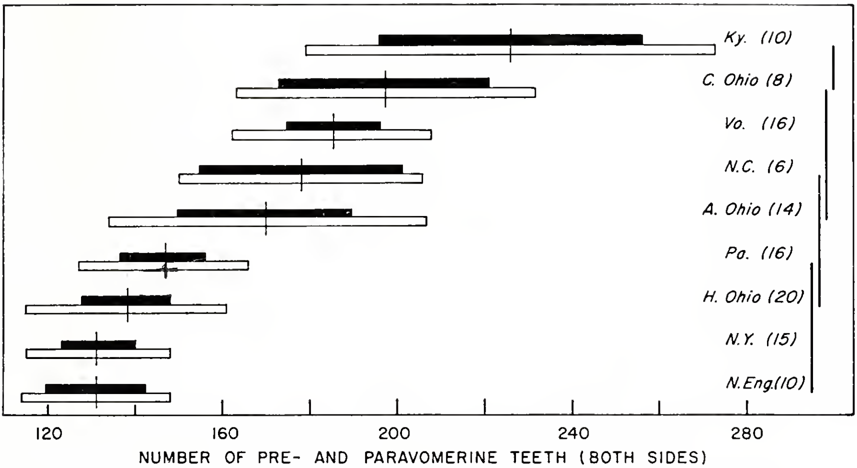

FIG. 9. Number of pre- and paravomerine teeth in *G. porphyriticus:* Data shown are means (vertical lines), one standard deviation (white bars), and two standard errors of the mean (black bars). Vertical lines on the right connect means of samples which are not significantly different (DMRT, $\alpha = 0.05$, $s = 9.52$). Sample size is in parentheses following locality. Localities are, from top to bottom: Carter Co., Ky.; Cincinnati, Ohio; Grayson Co., Va.; Burke Co., N.C.; Adams Co., Ohio; Pennsylvania; Hocking Co., Ohio; New York; New England.

than *p. porphyriticus.* In this one character, the Hocking Co., Ohio, *inagnoscus* resemble *p. porphyriticus,* Virginia and Cincinnati intergrades resemble *p. duryi.* As judged by this character, the Adams Co., Ohio, specimens should be considered intergrades between *p. porphyriticus* and *p. duryi.* In number of prevomerine and paravomerine teeth, *p. danielsi* is more like *p. duryi* than *p. porphyriticus.*

Statistical comparison of tooth counts from large numbers of specimens probably reliably indicates similarity or difference between populations, reflecting evolutionary relationships. However, counts have little value in identifying individual specimens because of great individual variation, much of which is real, but some certainly result from difficulties in counting individual teeth.

NUMBER OF PREMAXILLARY AND MAXILLARY TEETH

The number of premaxillary and maxillary teeth has not been used as a taxonomic character in *Gyrinophilus.* Rabb (1958, p. 35), analyzing taxonomic variation in maxillary teeth in *Chiropterotriton,* concluded that "dental features [should] be treated cautiously as taxonomic characters and . . . their relative weight may have to be adjusted or discounted in individual cases." These studies indicate strongly that dental features in *Gyrinophilus* have little or no value as subspecies recognition characters,

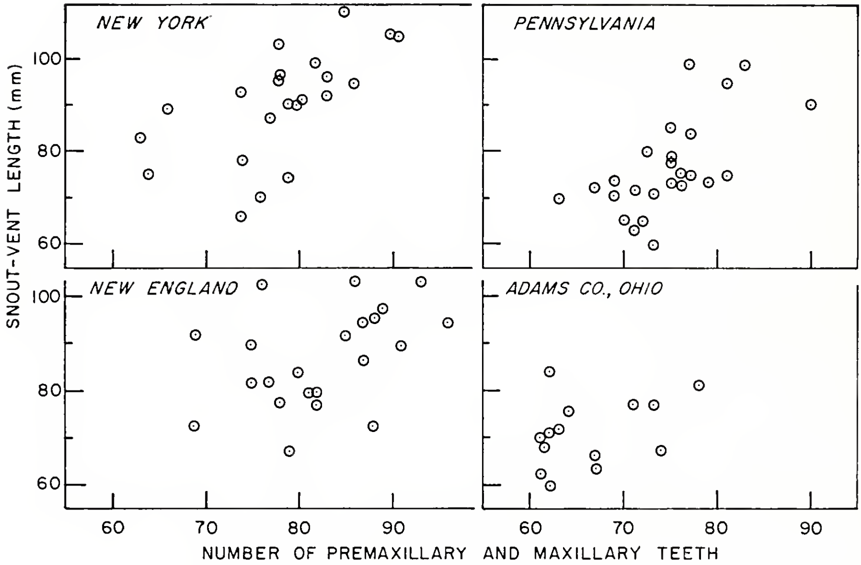

FIG. 10. Ontogenetic increase in number of premaxillary and maxillary teeth in *G. porphyriticus*.

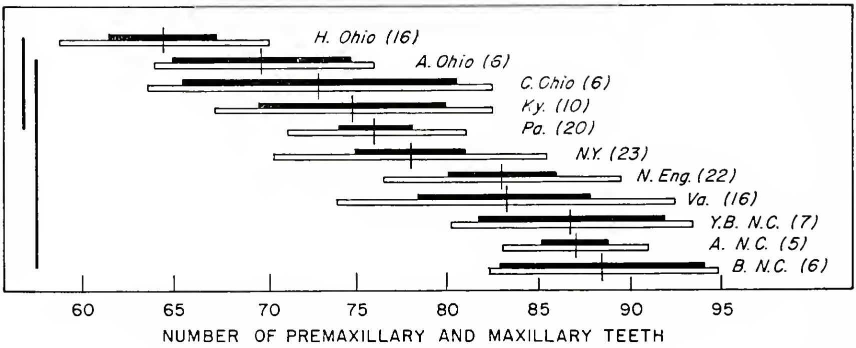

FIG. 11. Number of premaxillary and maxillary teeth in *G. porphyriticus:* Data shown are means (vertical lines), one standard deviation (white bars), and two standard errors of the mean (black bars). Sample size is in parentheses following locality. Vertical lines on left connect means of samples that are not significantly different (DMRT, $\alpha = 0.05$, $s = 10.4$). Localities are, from top to bottom: Hocking Co., Ohio; Adams Co., Ohio; Cincinnati, Ohio; Carter Co., Ky.; Pennsylvania; New York; New England; Grayson Co., Va.; Yancey and Buncombe counties, N.C.; Alleghany Co., N.C.; Burke Co., N.C.

but are of some use in analyzing possible evolutionary relationships among the subspecies, and their zoogeographical histories.

There is a demonstrable ontogenetic increase in number of these teeth (Fig. 10).

Because of the ontogenetic change in number of premaxillary and maxillary teeth, comparisons should be made between individuals of one particular size class. However, since there were only a few specimens available for each size class, not enough for a statistical sample, all specimens within a given size range (70–90 mm) were used. Fig. 11 summarizes results of counts of these two tooth series on specimens from the indicated areas.

Although there appears to be a trend toward more premaxillary and maxillary teeth in *p. porphyriticus* and the northeastern-most populations of *p. danielsi,* the only samples that are statistically different (0.05) are those from Hocking Co.. Ohio, and Burke Co., N.C.

NEOTENY

Neoteny (as applied to salamanders) is usually defined as "a situation in which sexual maturity is attained, even though the individual involved retains the external gills and other essentially larval features" (Tihen, 1958). The use of this concept implies that somewhere in the phylogenetic line of the form under consideration there was a metamorphosing ancestor (de Beer, 1958).

Within the salamander family Plethodontidae two monotypic genera are neotenic (*Typhlomolge* and *Haideotriton*), and two contain neotenic species (*Gyrinophilus* and *Eurycea*). In all cases in this family neoteny is associated with residence in or around caves. The neotenic *Gyrinophilus palleucus,* three species of *Eurycea,* and adult *Typhlotriton spelaeus* are restricted to caves; the remaining neotenic species of *Eurycea* and larval *T. spelaeus* are found in caves or around exits of springs and underground streams.

Although neoteny is associated with cave-dwelling in plethodontids, this relationship does not hold for neotenic members of other families found in North America. Some genera of other families containing neotenic species or local neotenic populations are: *Notophthalmus* (Salamandridae); *Ambystoma, Siredon, Dicamptodon, Rhyacotriton* (Ambystomidae); *Necturus* (Proteidae); *Amphiuma* (Amphiumidae); *Siren, Pseudobranchus* (Sirenidae); *Cryptobranchus* (Cryptobranchidae). In most of these neoteny is associated with adaptation to permanent dwelling in large streams, lakes, ponds, and swamps.

Neoteny in *Dicamptodon* seems to be an adaptation for permanent stream-dwelling when such streams are available; otherwise it transforms (Schuirer, 1958). Neoteny in *Ambystoma tigrinum* may have been of survival value in populations near glacier borders during the Pleistocene

(Tihen, 1958). Only in the European *Proteus* and the North American plethodontids is neoteny associated with adaptation to the peculiar environment found deep within caves.

Mechanisms involved in the production and maintenance of neoteny are not at all well understood for any one form, but indications are that several exist. Neoteny in *Ambystoma tigrinum* seems to be correlated with high altitude, low temperature, and perhaps iodine deficiency in environmental waters (Tihen, 1958). In the Mexican axolotl, *Siredon mexicanum,* either the thyroid-stimulating hormone (TSH) is not produced in adequate amounts or thyroxin never leaves the thyroid gland (Lynn, 1961). The tissues of *Necturus* and *Proteus* are not responsive to thyroxin and only certain tissues of *Cryptobranchus* and *Siren* are responsive. Among plethodontids *Typhlomolge rathbuni* and *Haideotriton wallacei* have been induced to undergo some metamorphic change under the influence of thyroxin (Dundee, 1957, 1962), but the result was usually fatal. Gorbman suggested (1957) that neoteny in *T. rathbuni* may result in part from decreased sensitivity of tissues to thyroxin, and in part to a reduced thyroid gland. Certain of the neotenic *Eurycea* have been induced to transform by treatment with thyroxin: *E. tynerensis, E. neotenes,* and *E. nana* (Kezer, 1952; Potter and Rabb, 1959). The actual cause of too little circulating thyroxin in the latter forms is unknown. Detailed experiments to induce metamorphosis in neotenic species capable of metamorphosing which take into account all the hormonal influences of normal metamorphosis will probably be of help in understanding the biochemical factors involved in the development and maintenance of neoteny. It appears, however, that neoteny is not an accidental occurrence, or even, in the majority of cases, a simple phenotypic response to environmental conditions; it is of survival value to those forms in which it occurs. Selection of any traits tending to reinforce the neotenic condition would be expected, and has resulted in the several different mechanisms observed in those forms studied. Four factors that might increase the survival value of neoteny in cave-adapted salamanders are: (1) dispersal through and living submerged in ground water, (2) most available food items in caves are aquatic, either cave-adapted aquatic invertebrates or such organisms washed in from the outside, (3) a relative scarcity of food in the cave environment, and (4) the correlative avoidance of the energy expenditure of metamorphosis.

Individuals of the neotenic species of *Gyrinophilus, G. palleucus,* consistently undergo metamorphic changes with thyroxin treatment (Dent *et al.,* 1955; Lazell and Brandon, 1962; Dent and Kirby-Smith, 1963). Thus a normally low level of thyroidal activity may prevent any metamorphic changes from occurring in nature (Dent and Kirby-Smith, 1963). However, experiments to induce metamorphosis by injections of thyroid-stimulating hormone, pituitary gland implantation, or the addition of iodides to aquarium water are inconclusive (Blair, 1961; Dent and Kirby-Smith, 1963).

The description of *G. palleucus* and the redescription of the allegedly neotenic *G. lutescens* (see section dealing with *p. duryi*) have led investigators of *Gyrinophilus* to postulate the occurrence of neotenic populations of *G. porphyriticus*. This impression of "incipient" neoteny in *porphyriticus* is perhaps fostered by the large size attained by many larvae prior to metamorphosis (e.g., Barr, 1961, p. 49).

I have seen only one specimen of *G. porphyriticus* that might mistakenly have been considered neotenic (AMNH 51637, Estill, Floyd Co., Ky., 82 mm long). The specimen is actually in metamorphosis and has stubby gills, fused premaxilla, maxillary teeth, modified prevomer, no paravomerine teeth, low tail fin, modified head shape, and a larval tongue. A radiograph shows that, although most of the skull is larval, the anterior bones have undergone some change from the larval condition. In the absence of data indicating neoteny in *porphyriticus* and in view of the partially metamorphosed condition of the specimen (AMNH 51637), I would consider that the specimen simply began transformation at an unusually large size. The ovaries contain numerous small, unyolked ova (0.27–0.67 mm in diameter). The presence of small ovarian ova in larval specimens does not indicate neoteny (Wilder, 1925).

SYSTEMATIC TREATMENT OF INCLUDED FORMS

GYRINOPHILUS PORPHYRITICUS (GREEN)

Salamandra porphyritica Green, 1827:3.

Salamandra salmonea Storer, *in* Holbrook, 1838:101–102, pl. 22 (Green Mountains, Vermont; no known type-specimen) (a junior synonym of *S. porphyritica* Green, 1827, as suggested by Baird, 1850:287).

Pseudotriton salmoneus: Baird, 1850:287–288 (noted that *P. salmoneus* is probably *S. porphyritica* of Green and that *S. porphyritica* may be an *Ambystoma*).

Spelerpes [?] *salmonea* [*sic*]: Gray, 1850:46 (noted that this is probably the same as *S. porphyritica* Green, 1827).

Spelerpes [?] *porphyritica* [*sic*]: Gray, 1850, *loc. cit.*

Ambystoma salmoneum: Duméril, Bibron, and Duméril, 1854:110 (transferred *S. salmoneum* Storer, 1838, to *Ambystoma* Tschudi, 1838, presumably on the basis of Baird, 1850, *loc. cit.*).

Spelerpes salmoneus: Cope, 1866:98 (transferred *S. salmoneus* Storer, 1838, to *Spelerpes* Rafinesque, 1832).

Gyrinophilus porphyriticus: Cope, 1869:108–109 (described the genus

Gyrinophilus, type-species *Salamandra porphyritica* Green, 1827, by monotypy, distinguishing it from *Spelerpes*).
Geotriton porphyritica: Garman, 1884:40 (transferred *S. porphyritica* Green, 1827, to *Geotriton* Bonaparte, 1831).

Remarks. Hallowell's citation of *Ambystoma porphyriticum,* to judge by his description, is clearly not *S. porphyritica* Green, 1827. Boulenger (1882) placed (probably correctly) *A. porphyriticum* in the synonymy of *A. microstomum* (*A. texanum*).

DeKay's (1842) description and figure of *Triton porphyriticus* refer not to *S. porphyritica* Green, 1827, but probably to *Plethodon glutinosus* as indicated by Hallowell (1856:9). Holbrook's (1842, vol. 5, p. 83, pl. 28) citation of *Triton porphyriticus* likewise does not refer to *S. porphyritica* Green, 1827.

Content. Four subspecies are recognized: *G. p. porphyriticus, p. duryi, p. danielsi,* and *p. dunni.*

Diagnosis. G. porphyriticus differs from *G. palleucus* in that it naturally metamorphoses from an aquatic larva dwelling in springs or small streams into a semiterrestrial adult which lacks gills, has a canthus rostralis, develops eyelids, loses the caudal fin, and undergoes the cranial changes already discussed (pp. 8–11). *G. palleucus* is neotenic.

Eyes of larval *G. porphyriticus* are larger than those of *G. palleucus,* tooth counts are lower, and the head is not so broad, flat, and spatulate.

Canthus rostralis. The canthus rostralis (Fig. 12) (Greek *kanthos,* corner of eye, plus the Latin *rostralis,* of, on, in the beak, snout) has been used as a character for identifying *Gyrinophilus porphyriticus* since Green's description (1827, p. 3) of *Salamandra prophyritica,* in which he noted, "a slight ridge, formed by the superior part of the upper maxillary bone, extending from the anterior angle of the eye to the nostril. . . ."

In his description of the genus *Gyrinophilus* (1869), and later (1889), Cope described the external appearance of the canthus rostralis as characteristic of the genus (monotypic at that time). Although the degree of development of the canthus rostralis varies considerably in the subspecies of *G. porphyriticus,* its presence on metamorphosed individuals is universal and unique.

The canthus is most evident on *p. danielsi* and *p. dunni,* moderately well developed on *p. porphyriticus,* and usually poorly developed on *p. duryi.*

Since the canthus is characteristic of and restricted to the genus, its actual structure was examined. Heads of adult *p. porphyriticus* (Nelson Co., Va.), *p. duryi* (Carter Co., Ky.), *Pseudotriton ruber* (Frederick Co., Md.), *P. montanus* (Fayette Co., Ky.), and *Ambystoma texanum* (Urbana, Ill.) were serially sectioned and examined.

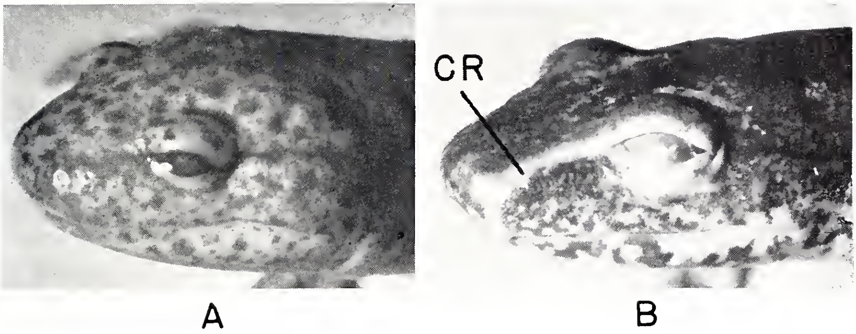

FIG. 12. A. *Pseudotriton ruber* head showing lack of the canthus rostralis; B. *Gyrinophilus porphyriticus* head showing canthus rostralis (CR).

There is no bony ridge associated with the canthus, or any other tissue that was not present in the *Pseudotriton* and *Ambystoma* examined. In all specimens of the three genera the region occupied by the canthus in *Gyrinophilus* contains a thickening of the subintegumentary connective tissue through which run tubules of the "superficial olfactory gland" (Hilton, 1951). The tubules lie on the dorsal surface of the nasal bones.

The canthus rostralis seems to result from (1) a relatively wider, more truncate snout which is, however, no more acutely angled laterally than in other forms examined, and (2) the distinctive nonpigmented line running along the lateral margin of the snout, which is usually emphasized by darker, bordering pigment. The canthus is primarily a pigmentary feature, emphasized by the shape of the snout and slightly swollen ciral regions at the labial ends of the nasolabial grooves.

Gyrinophilus porphyriticus porphyriticus (Green)

Salamandra porphyritica Green, 1827:3.
Gyrinophilus porphyriticus: Cope, 1869:108–109.
Gyrinophilus porphyriticus porphyriticus: Stejneger and Barbour, 1933:15.
Gyrinophilus porphyriticus inagnoscus Mittleman, 1942:27–30, pl. VIF (Holotype USNM 115520, Salt Creek, 4 miles southwest of South Bloomingville, Salt Creek Twp., Hocking Co., Ohio, as corrected by Condit, 1958).

Type and type-locality. Dunn (1926, p. 26) noted that the type of *G. p. porphyriticus* is "Not known to exist." Green's description and figure of *S. porphyritica* adequately identify his material, collected "in French Creek, near Meadville, Crawford County, Pa.," with the form now known as *G. p. porphyriticus,* but the only indication of particular specimens examined by him is found in his phrase on page 3, "Cabinet of the Maclurian Lyceum—my collection." The Maclurian Lyceum was a short-lived society organized in Philadelphia in 1826 to promote knowledge of the arts and sciences by formation of a cabinet and library, the holding of meetings, and publication of a journal (Weiss and Ziegler, 1931; and the introduction to 1(1), *Contr. Maclurian Lyceum,* 1827). Only three issues of the *Contributions* appeared, these between January 1827 and January 1829.

I have tried without success to locate specimens of S. *porphyritica* that Green may have had in his personal collection. Apparently part or all of the surviving Green collection was acquired by the Academy of Natural Sciences of Philadelphia. H. W. Fowler (personal communication) informed me that no specimen of *Gyrinophilus* was among the acquisition. Green taught at Jefferson College at Canonsburg, Pa. (now part of Washington and Jefferson College, at Washington, Pa.), and at the Jefferson Medical College of Philadelphia about the time S. *porphyritica* was described. I wrote to both these institutions inquiring about preserved specimens there now. No answer was received from the former; the latter had no record of the Green specimens, but referred me to the College of Physicians of Philadelphia. W. B. McDaniel, 2nd, Curator of the Library Historical Collections of the latter institution, informed me that their Mütter Museum contains none of Green's material, and that available bibliographical accounts of Green offered no clue as to the deposition of his specimens. There is little likelihood that Green's specimens of S. *porphyritica* are still in existence.

As far as I can determine, the only extant specimens of earlier collections from the type-locality of S. *porphyritica* are USNM 3852 (six specimens). These six are badly macerated and completely unsuitable for taxonomic determinations.

In keeping with Article 75 of the International Code of Zoological Nomenclature, 1961, the following recently collected specimen is designated neotype of *Gyrinophilus porphyriticus porphyriticus* (Green, 1827) (Fig. 1A).

Neotype. MCZ 35778, male, collected 15 April 1962, by J. D. Lazell, Jr., and L. M. Lazell in a small spring-fed stream (flowing directly into French Creek) at Liberty and Linden streets, Meadville, Crawford Co., Pa.

Description of neotype. Male, 18 trunk vertebrae (17 costal grooves); measurements taken one day after fixation in 10 per cent formalin—head width just behind eyes, 17.7 mm; snout to gular fold mid-ventrally, 21 mm; snout-anterior margin of vent, 105 mm; snout-posterior margin of vent, 113 mm; posterior margin of vent to tip of tail, 67 mm; distance from axilla to groin, 64 mm; canthus rostralis interrupted near anterior end of snout by dark pigment, continuous in nasolabial groove region; lower eyelid clear, upper darkly pigmented; dorsum and sides above upper limb insertion covered by brown and black mottlings—black pigment especially pronounced on dorsum of head and forelimbs, and a pair of patches on the anterior third of trunk; entire ventral surface flesh colored and heavily covered with fine dark flecks (color notes were taken from the specimen in life).

Diagnosis. A metamorphosing *Gyrinophilus* with darkly mottled or reticulated dorsum, differing from *p. duryi* and *p. dunni* by the presence of numerous melanophores on belly of large specimens; from *p. duryi* by a more distinct canthus rostralis; from *p. dunni* and *p. danielsi* by a less distinct canthus rostralis, anterior convergence of the paravomerine tooth series, and nearly straight transverse portion of prevomerine tooth series; and from *p. duryi, p. danielsi,* and *p. dunni* by lacking (except in New England and Canadian populations) distinct black spots dorsally and laterally.

Pattern variation. Within this subspecies there are several striking pigmentary features that are characteristic of certain areas and show up with lowered frequency in other areas. These features are possibly the result of one or more of the following: (1) genotypic variation through action of local selective pressures, (2) genotypic variation through random drift in small, isolated populations, (3) phenotypic response to local conditions. Any of these factors would be affected by increasing human activity (deforestation, water pollution, etc.). The inheritance and heritability of these features have not been investigated, but none is sufficient for nomenclatural designation. They are included here only to give a more complete picture of phenotypic (and perhaps geotypic) diversity in this form.

Dorsal and lateral black markings appear to have arisen independently in populations of *p. porphyriticus* at the northern extremity of the range and at its southwestern limit, completely separated by intervening unspotted populations in northern Ohio, Pennsylvania, northern West Virginia, Maryland, and New York. Black dorsal and lateral dots in *p. porphyriticus* in southern Ohio, West Virginia, and Virginia result from intergradation with *p. duryi.* A different sort of marking appears in New England and Canadian populations. Here the dark larval reticulations along the sides and back tend to become intensified in adults. On some specimens (e.g., UM 25–6–16–3, Hampshire Co., Mass.) the reticulations are moderately darkened and broken into segments along the sides and tail. On AMNH 44727–36 (South Waterford, Me.) dark pigment (especially evident on smaller specimens) extends ventrally in the costal grooves forming broken black lines on the lower sides. Individual black dots are scattered along the sides and throat just ventrad of the lateral limit of dorsal ground color. On others (e.g., USNM 129383–6, Stockbridge, Vt.) numerous small black segments and dots (Fig. 2B) obviously originate from reticulations. On NMC 2862 (Glen Sutton, Quebec) the relationship of lateral and dorsal dots to the larval reticulations is not at all apparent, but it is assumed to exist.

The black dots of *p. duryi, p. danielsi,* and *p. dunni* do not appear to result from retention of part of the larval reticulations (in fact the larvae are more dotted than reticulated), but from the accumulation of pigment in different areas.

The retention of larval reticulations in an unmodified to slightly hypertrophied form is characteristic of young adults in some parts of New York and Pennsylvania. Three specimens from Cattaraugus Co., N.Y., provide serial demonstration of the usual development of adult pigment in most parts of New York and Pennsylvania. A specimen 83 mm in length has a 4-mm–wide mid-dorsal band of rather uniform pigmentation which spreads out anteriorly and covers the dorsal surface of the head. The sides of the body, head, and tail are covered by larval reticulations. Unpigmented spots (1.25-mm diameter) conspicuously enclose each lateral sensory pore on the body and tail. Larval reticulations are restricted to the lower tail and sides of an 88-mm specimen. The upper surface of the tail and back is irregularly mottled to the level of the lateral sensory pore row. The reticulated pattern on the back has been nearly obscured by interreticular pigment. All of the reticulated pattern, except faint traces along its ventro-lateral margin, is gone on a 93-mm specimen. The back, and dorsum of the head and tail, are uniformly dark, except for a distinctly chevronate pattern of pigment mid-dorsally. Pale spots enclosing lateral sensory pores are small (1-mm diameter) and are even smaller on larger specimens (0.5 mm). The general ground color becomes increasingly darker on larger specimens.

Adults of certain Pennsylvanian populations characteristically retain large, pigmentless spots enclosing the lateral sensory pores (e.g., UMMZ 68638–9, 68641, Warren Co.).

Some difference was noted between New England and Canadian, and more southern populations of *p. porphyriticus,* in the ventrolateral extension of the dark dorsal ground color. On South Waterford, Me., specimens (71–102-mm long), for example, the dorsal ground color ends at, or often above, the level of the upper limb insertion. On Broome Co., N.Y., specimens (73–107 mm) the dorsal ground color always extends to the mid- or lower limb insertion.

Mittleman (1942) considered the formation of a chevron-like pattern of spots and flecks along the median dorsal line a diagnostic character of *inagnoscus* but it is not restricted to the supposed range of *inagnoscus.* Chevronate patterns can result from two different features acting separately or jointly, the accumulation of small dark flecks and dots along and in fine anterodorsal extensions of costal grooves or from the hypertrophy of the extensions themselves, and of the folds between them. The latter are not merely fixation phenomena. The effect is most striking when the two features are superimposed (as on most Hocking Co., Ohio, specimens; Fig. 2A).

Chevronate patterns were observed on specimens from Canada (two of four specimens P); New England (5–7–0–39); New York (18–11–1–108); Pennsylvania (27–2–0–45); Maryland (1–0–0–10); northeastern Ohio (36–4–18–20); West Virginia (8–21–1–66); Cincinnati, Ohio (45–0–0–9); and Hocking Co., Ohio (25–0–60–21). The numbers in parentheses refer, in order, to: percentage of specimens having pigmentary chevrons (P), percentage of morphological chevrons, percentage of both pigmentary and morphological chevrons, sample size. Chevronate patterns were also observed in North Carolina *p. danielsi* (14 per cent of 69 specimens), Tennessee *p. danielsi* (10 per cent of 47 specimens), and most large *p. dunni*.

Specimens examined.

CANADA: *Ontario:* Brittania (NMC 2308); opposite Buffalo (MCZ 1370). *Quebec:* between Bolton Centre and Knowlton (NMC 5073); west side of Foster Mountain, northeast of Knowlton (NMC 5072, 5074); Glen Sutton (NMC 2856, 2862); Iron Hill (NMC 2118, 2684); 2 miles south of Knowlton Landing (NMC 2871); 3 miles north of Waterloo (NMC 2840).

CONNECTICUT: *Tolland Co.:* Storrs (USNM 27746).

MAINE: *Cumberland Co.:* Camp Wigwam, Harrison (CNHM 91153); Harrison [?] (CNHM 91152). *Oxford Co.:* South Waterford, Mutiny Brook and tributary (AMNH 44727–36); South Waterford, Mutiny Creek (UMMZ 122746); near South Waterford (AMNH 18801).

MARYLAND: *Allegany Co.:* Cumberland (USNM 141317). *Garrett Co.:* southeast of Grantsville (UMMZ 89855); Jennings (ANSP 18389, 18393); Mountain Lake Park (OUVC 3918; UIMNH 50133–4); Mt. Inn, near Frostburg (CM 4759); Savage River (USNM 101983); Solomon's Ridge (USNM 102174–7); White's Knob (USNM 101889–90, 102188).

MASSACHUSETTS: *Berkshire Co.:* Mt. Washington (ANSP 45090–2); Williamstown (MCZ 4483, 4486, 4488, 8822; UMMZ 53009–11). *Hampshire Co.:* Holyoke Twp. (UM 25–6–16–2); Williamsburg Twp. (UM 25–6–16–3). *Worcester Co.:* Princeton (MCZ 2296).

NEW HAMPSHIRE: *Cheshire Co.:* Jaffrey (MCZ 5630); near Keene (UMMZ 86229); Mt. Monadnock State Park (BDV). *Grafton Co.:* Franconia Notch, Flume Brook (CM 6182–3); (UMMZ 86228). *Merrimack Co.:* (UMMZ 84532). *Uncertain locality:* White Mountains (MCZ 996).

NEW JERSEY: *Sussex Co.:* Sparta (USNM 123937). *Union Co.:* Plainfield (MCZ 4489). *Warren Co.:* Pahaquarry Copper Mine (CU 4253); (AMNH 53620).

NEW YORK: *Albany Co.:* Clarksville (CNHM 91161); Dolder's Swamp, near Voorheesville (CNHM 91157); Indian Ladder, Albany (CNHM 91158–9); Thatcher Park (CNHM 91160); Voorheesville (CNHM 7049; NCSM 7626); near Voorheesville (CNHM 91155–6). *Allegany Co.:* between Friendship and Richburg (CNHM 93231, 93233–6). *Broome Co.:* Binghamton (CM 21722; CU 4026, 4086, 5615). *Cattaraugus Co.:* Allegany State Park (CNHM 91164–6, 91175–202, 91203–12, 93237–8); Haskell Creek (CM 30350). *Cayuga Co.:* near Locke (TU 15266). *Chemung Co.:* Horseheads (CU 6455). *Chenango Co.:* [?] (ANSP 10565). *Cortland Co.:* Beaver Brook, Gracie (CNHM 91213–23); Beaver Creek (CU 4048); near Marathon [?] (CNHM 91154). *Delaware Co.:* 1.5 miles east of Downsville (CNHM 91226–36); 2 miles east of Downsville (UMMZ 78863); Stamford (CNHM 91124–5). *Erie Co.:* 3 Valley Nature Reserve, Holland (CNHM 91237–8). *Essex Co.:* Minerva (USNM 123962). *Franklin Co.:* Tupper Lake (MCZ 4274). *Genesee Co.:* Letchworth Park (CNHM 91239). *Herkimer Co.:* Mohawk (CM 1665). *Jefferson Co.:* Woodville, Canadaigus Lake (CNHM 91240). *Orange Co.:* Pochuck River, Newport (CNHM 91242). *Rensselaer Co.:* east of Troy (CNHM 91248). *Steuben Co.:* Arkport (CNHM 91244–6); 1 mile south of East Corning (CNHM 91248). *Tioga Co.:* Barton Twp. (CU 4736); Berkshire (MCZ 1240, 4577–8). *Tompkins Co.:* Chicago Bogs, McLean Wildlife Preserve, Ithaca (CNHM 91249); Connecticut Hill, near Ithaca (BDV); Ithaca (USNM 39404); 9 miles east southeast of Ithaca, Statersville Nature Preserve (UMMZ 120340–1). *Ulster Co.:* vicinity of Montelo (UMMZ 81745). *Warren Co.:* Lake George (USNM 80212–4). *Washington Co.:* eastern shore of Lake George, opposite Hague (CNHM 91251). *Yates Co.:* 4 miles southwest of Middlesex (USNM 115373–4). *Uncertain locality:* Catskills (USNM 23181); Adirondack (USNM 3842); McBride Pond, Adirondack Mountains (MCZ 3967); central New York (ANSP 10434).

OHIO: *Ashland Co.:* Mohican State Park (OSM 520). *Knox Co.:* Brinkhaven (OSM 189.25, 4372.9–.14); near Brinkhaven (CNHM 1876); Gambier (CNHM 36613).

PENNSYLVANIA: *Armstrong Co.:* Big Run, Franklin Twp. (UK); Dicky Run, Franklin Twp. (UK). *Berks Co.:* near Port Clinton (UIMNH 50477). *Blair Co.:* Altoona [?] (ANSP 513). *Bradford Co.:* Barkley Mountain, Franklindale (CNHM 91252–5); Windham (MCZ 1000). *Chester Co.:* near Marshallton (JDL). *Clarion Co.:* Foxburg (USNM 3841, 3847). *Clinton Co.:* 5 miles north of Round Island (ANSP 4590–2). *Crawford Co.:* Meadville (MCZ 35778; USNM 3852). *Cumberland Co.:* Carlisle (USNM 3874, 8266, 14468, 131633–6). *Indiana Co.:* Homer (ANSP 26429); Indiana (ANSP 18692–3, 18921, 21363–7, 21368, 26508, 26535); 12 miles south of Indiana (ANSP 26516, 26520); Ramsey Run

(ANSP 22033). *Lycoming Co.:* Armstrong Twp., Haggerman's Run (UMMZ 98098, 98102); Plunketts Creek Twp. (UMMZ 98099). *McKean Co.:* Port Allegany (ANSP 16240; CNHM 7050, 91256–8, 91260; USNM 67106). *Monroe Co.:* Pocono Lake Preserve (ANSP 55347). *Potter Co.:* 8 miles north of Galeton (CU 5318). *Somerset Co.:* (USNM 57358). *Susquehanna Co.:* 0.7 mile south of Hop Bottom, junction of routes 11 and 167 (BDV). *Tioga Co.:* Ansonia (CU 5326); Blossburg (AMNH 22546–9). *Warren Co.:* near Atkins Farm (UMMZ 68637); Brown River (UMMZ 68639); Irvine Run (UMMZ 68642); Morrison Run (UMMZ 68641). *Washington Co.:* Canonsburg (USNM 3840). *Wyoming Co.:* Monroe Twp. (ANSP 64725–8). *Uncertain locality:* Mosgrove (UK); 1 mile south of Russell (UMMZ 68640); between Shipman's Eddy and Big Bend (UMMZ 68638); Two Lick Hills (USNM 99032); Warr (UMMZ 99331); (ANSP 22659–61, 22662, 22774).

VERMONT: *Addison Co.:* Granville (ANSP 50843). *Bennington Co.:* near Searsburg (CM 21612). *Chittenden Co.:* Underhill (CM 22814). *Lamoille Co.:* 2.5 miles west southwest of Stowe (USNM 108703). *Rutland Co.:* 3 miles west of Wallingford, Balestra Farm (UMMZ 109212). *Windsor Co.:* Stockbridge (MCZ field ser. 12818–20; USNM 129383–6).

VIRGINIA: *Alleghany Co.:* 1.5 miles north northwest of Clifton Forge (CM 22902). *Augusta Co.:* Blue Ridge Parkway (UFl 6981); Luray Caverns (USNM 141514); Shenandoah National Forest (UMMZ 122589). *Amherst Co.:* Washington National Forest, Mt. Pleasant area, Rocky Mount (UMMZ 122747). *Bedford Co.:* near Blue Ridge Parkway milepost 80 (GRT 1278). *Highland Co.:* 3 miles east of Monterey, spur of Jack Mountain (CM 5689). *Nelson Co.:* Midway (MCZ 5628, 7323); 1.8 miles east of Montebello (UIMNH 50478). *Page Co.:* Stony Man Mountain (USNM 31627, 35885). *Roanoke Co.:* Stanley Cave (DU A616). *Rockingham Co.:* Big Run at 1500 feet (USNM 140347); Harrisonburg, Rawley Springs (CM 16349). *Uncertain locality:* Upper James River (USNM 3878).

WEST VIRGINIA: *Barbour Co.:* Elk Creek (OUVC 3478). *Berkeley Co.:* between Berkeley Springs and Martinsburg (AMNH 43665). *Greenbrier Co.:* Organ Cave (TCB); Unus Cave (WVBS 2455). *Harrison Co.:* Liberty, 3 miles north of Clarksburg (WVBS 2183); (WVBS 2410). *Lewis Co.:* Weston (WVBS 2184). *Pocahontas Co.:* Big Spring Run (USNM 33624); Bartow (OUVC 3037–40, 3894–5); Durbin (AMNH 40139–42); Raine's Cave (WVBS 1186); Snedegar's Cave (TCB); Tub Cave (MCZ 27026); Watoga State Park (NCSC). *Preston Co.:* mountain stream into Lake Terra Alta (UMMZ 72289); Little Laurel Creek, field #1 (WVBS 1905); Pisgah (WVBS 2103); Terra Alta (UK). *Randolph Co.:* near Alpena (UFl 6998); Cheat Bridge (BDV); between Cheat Mountain and Guadineer Knob (OUVC 2600); Elkins (WVBS 791, 1110);

Files Creek, Cheat Mountain cove (USNM 33612); Hermit Cave (USNM 110937–8); Kumbrabow State Forest, field #1 (WVBS 1902–3); (WVBS 2104). *Tucker Co.:* Backbone Mountain, field #1 (WVBS 1915); Monongahela National Forest, 2 miles southwest of St. George (OUVC 3479).

Alabama populations. Specimens from extreme northwestern Georgia, northern Alabama, and the single available specimen from northeastern Mississippi are similar to *p. porphyriticus* in dorsal pigmentation (Fig. 2C). They are usually dotted ventrally as is *p. porphyriticus* and are darkly mottled dorsally. The canthus rostralis is less distinct than in *p. porphyriticus* from northeastern states and is more like that of *p. duryi.* Along the lower sides are numerous tiny flecks as in *p. dunni.* As shown in a previous section, the shape of the pre- and paravomerine tooth series is most similar to *p. dunni.*

A series of specimens from the vicinity of Tuscaloosa, Ala., at the southwestern-most limit of the species range, is characterized by great variation in pigmentation. The largest specimen (105-mm snout-vent), except for a less distinct canthus, resembles specimens from Maine. It is darkly mottled dorsally, and the dark pigment extends only as far ventrally as the upper limb insertion. Smaller specimens from the Tuscaloosa area have a variable number of dark dots showing through the dorsal ground color (Fig. 2D). Two juvenile specimens (UIMNH field ser. 2253, 64-mm snout-vent; UIMNH field ser. 1916, 60-mm snout-vent) from a small ravine near Lock 13 of the Black Warrior River, are reminiscent of juvenile specimens from Cincinnati, Ohio. The canthus rostralis is moderately distinct and a pronounced dorsolateral row of black dots runs from the head onto the tail, in *p. duryi* fashion. A larger specimen from the Lock 13 locality (UIMNH field ser. 1917, 93-mm snout-vent) resembles adults from parts of eastern West Virginia, and would be considered an intergrade between *p. porphyriticus* and *p. duryi.*

It is impossible to assign a simple subspecific identification to the specimens from most parts of Alabama. Populations on Mt. Cheaha, in Talladega and Clay counties, closely resemble *p. dunni.* Those in extreme northern counties closely resemble *p. porphyriticus.* Other populations in Alabama appear to result primarily from *p. porphyriticus* with admixed genetic material from *p. dunni* to the east and from *p. duryi* to the north. The overlap in characteristics between *p. porphyriticus* and *p. duryi,* then, extends from eastern Ohio to the Fall Line in Alabama.

Specimens examined.

ALABAMA: *Bibb Co.:* 1.5 miles south of Marvel (RM). *Blount Co.:* North of Warrior (GRT 218). *DeKalb Co.:* Ft. Payne (TCB); 2.1 miles north of Ider (RM). *Jackson Co.:* Long Island Creek, 3 miles southwest of Higdon (BDV). *Lamar Co.:* Stuck's Springs (BDV). *Lawrence Co.:*

Bankhead National Forest, King Cove (BDV). *St. Clair Co.:* McLendon's Cave (TCB). *Shelby Co.:* 7.2 miles southwest of Helena (RM); 2 miles northeast of Montevallo (RM). *Tuscaloosa Co.:* just across Black Warrior River north of Tuscaloosa (UIMNH field ser. 2067, 2246); Lock 13, Black Warrior River, near Peterson (BDV; RB 835; UIMNH field ser. 1916, 1917, 2253, 2255, 2256); Lock 14, Tuscaloosa (TU 4948); 5.7 miles north of Windham Springs (BDV). *Winston Co.:* Black Warrior Forest (CM 21011–13, 22166).

GEORGIA: *Dade Co.:* Cloudland Canyon State Park (RB 769, 809); Lookout Mountain (MCZ 34108).

MISSISSIPPI: *Tishomingo Co.:* Tishomingo State Park (DEF).

Status of p. inagnoscus (Fig. 2A). Mittleman (1942) applied a new subspecific name, *inagnoscus*, to populations of *G. porphyriticus* in eastern and southeastern Ohio. The holotype of this form (USNM 115520) was collected at Salt Creek, 4 miles southwest of South Bloomingville, Salt Creek Twp., Hocking Co., Ohio (as corrected by Condit, 1958). Several of the paratypes were listed by OUZ numbers (Ohio University, Department of Zoology), but the specimens are no longer in that collection. The following specimens were located in the University of Illinois Museum of Natural History: UIMNH 36173–5 (OUZ 383–5); UIMNH 36176 (OUZ 916); UIMNH 36177 (OUZ 1230).

The essential points in the original diagnosis of *p. inagnoscus* were: distinguished from *p. porphyriticus* by (1) head narrower, less spatulate, (2) snout less truncate and rounder, (3) choanae very large, ovate or rounded, not minute and/or cuneiform, (4) parasphenoids well separated, more widely divergent posteriorly, (5) vomerine series short, heavy, more sharply angulated with the parasphenoids, (6) tail proportionally longer, (7) dorsal pattern usually uniformly mottled, with spots and flecks forming a chevron-like pattern medially, (8) venter pale, often pinkish, (9) ventral stippling finer and more sparsely distributed, and (10) orbitolabial stripe finer.

Several of the differences (1,2,7,8,9,10) would be expected in intergrade populations between *p. porphyriticus* and *p. duryi*. Others require further explanation (3,4,5,6).

The choanae of all specimens of *G. porphyriticus* examined were oval or circular in outline. The bony choana always appeared circular on radiographs. Occasionally a choana was partially filled with food material, detritis, or was partially filled in by swollen tissues bordering it, and in some of these instances appeared to be minute. Choanal diameter was measured on a number of specimens from throughout the range of the species, and the results are summarized in Fig. 13. Choanal diameter did not increase appreciably with an increase in head width or snout-vent length. The range of mean choanal diameters of the sample (0.42–

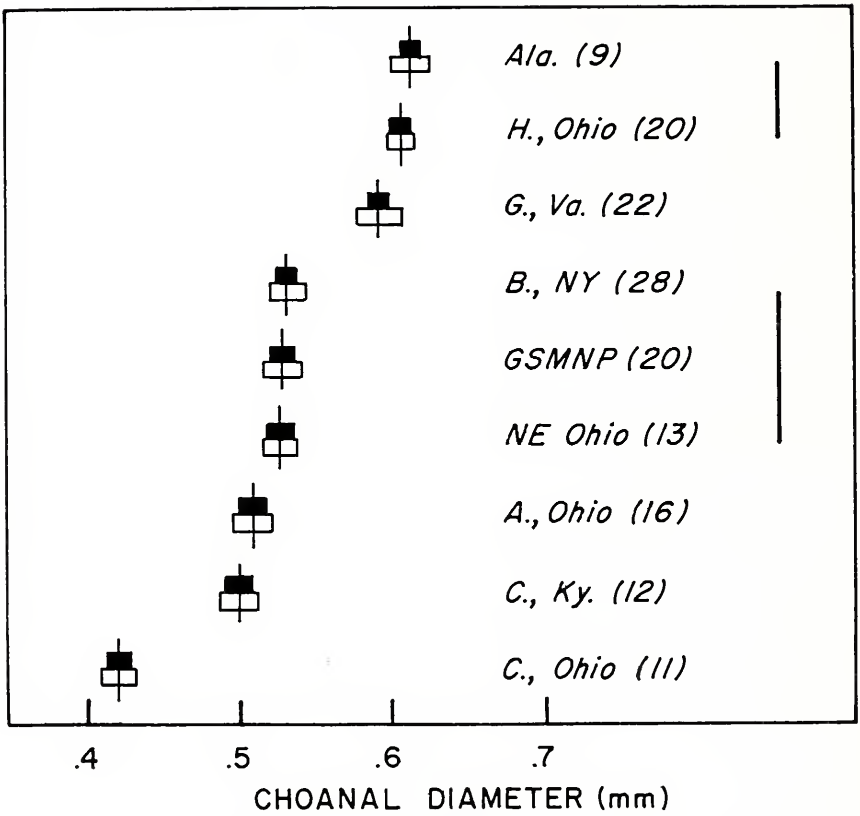

FIG. 13. Choanal diameter in *G. porphyriticus:* Data shown are means (vertical lines), one standard deviation (white bars), and two standard errors of the mean (black bars). Vertical lines on the right connect means of samples that are not significantly different (DMRT, $\alpha = 0.05$, $s = 0.012$). Sample size is in parentheses following locality. Localities are, from top to bottom: Alabama; Hocking Co., Ohio; Grayson Co., Va.; Broome Co., N.Y.; Great Smoky Mountains National Park; northeastern Ohio; Adams Co., Ohio; Carter Co., Ky.; Cincinnati, Ohio.

0.61 mm) was not large enough to justify use of the adjectives "minute" and "very large." Hocking Co., Ohio, specimens did have the largest choanal diameter, but those of New York specimens were only slightly smaller. The smallest choanal diameter was observed in the Cincinnati sample.

The shapes of the pre- and paravomerine tooth series were shown to be no different from those found in *p. porphyriticus.*

The frequency with which parts of tails are lost makes analysis of differences in relative tail length very difficult. Fig. 14 compares tail lengths

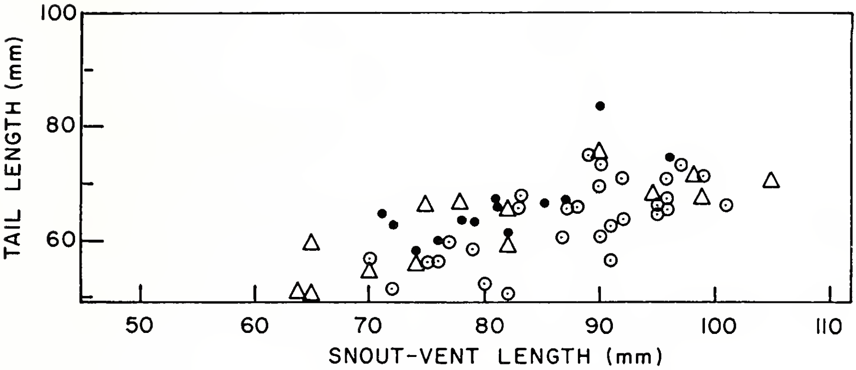

FIG. 14. Relative tail length in *G. porphyriticus:* New York (open circles); Pennsylvania (triangles); Hocking Co., Ohio (solid circles).

of *p. porphyriticus* from New York, Pennsylvania, and Hocking Co., Ohio. Although the tails of most Hocking County specimens were slightly longer than those of specimens of like length from New York, there was no difference between lengths of tails of Hocking County and Pennsylvania specimens.

Although *inagnoscus* does appear to be more extreme than either *p. porphyriticus* or *p. duryi* in some regards (extreme development of the dorsal chevronate pattern; highest incidence of specimens with 19 trunk vertebrae in *G. porphyriticus;* larger choanae; low number of premaxillary and maxillary teeth), in many others it appears to represent intergradation between *p. porphyriticus* and *p. duryi* (ventral pigmentation; dorsal and lateral dark dots on a mottled background; shapes of pre- and paravomerine tooth series; number of pre- and paravomerine teeth; moderately indistinct canthus rostralis). As was noted by Seibert and Brandon (1960), the greatest development of traits considered distinctive of *G. p. inagnoscus* occurs in Hocking and western Athens counties, Ohio. Although specimens from other counties do show these traits, such specimens appear to be reduced in frequency. It is clear that *inagnoscus* is in part the result of intergradation between *p. porphyriticus* and *p. duryi.* In view of the previously demonstrated variability within the subspecies *porphyriticus,* it would be inconsistent to use those traits which demonstrate some past (and perhaps present) differentiation in the populations in southeastern Ohio to justify subspecific status. A clearer picture of the relationships between the subspecies is obtained by considering southeastern Ohio populations intergrades between *p. porphyriticus* and *p. duryi* in an area which had previously been isolated sufficiently for some genetic change to have occurred. The present intergradation seems to be dispersing and diluting the distinctive features found in this isolated area. The occurrence in the intergrades of extremes not found in either presumed parental group is characteristic of, and expected in, intergrade populations arising from secondary contact of formerly disjunct populations.

Gyrinophilus porphyriticus duryi (Weller)

Triturus lutescens Rafinesque, 1832:121.
Pseudotriton duryi Weller, 1930:[6–9].
Gyrinophilus duryi: Weller, 1931:8.
Gyrinophilus porphyriticus duryi: Stejneger and Barbour, 1933:15.
Gyrinophilus danielsi duryi: King, 1939:556.
Gyrinophilus lutescens: Mittleman, 1942:33–35, pl. Vc.

Lectotype. Female, USNM 84300 (designated by Walker and Weller, 1932), collected 6 April 1930, by R. Dury and W. H. Weller.

Type-locality. Cascade Caverns, near Grayson, Carter Co., Ky.

Paralectotypes. Six topotypes mentioned by Weller (1930), and identified by Cincinnati Society of Natural History numbers 499 a-c, e-g. Two of these specimens are known to be in other collections now (MCZ 17540; CM 10937). The other four have not been located. They are no longer in the CSNH collection (now a part of the University of Cincinnati collection).

Diagnosis. G. p. duryi (Fig. 1B) was well distinguished from *p. porphyriticus* and *p. danielsi* by Walker and Weller (1932, p. 82): ". . . *duryi* differs from *porphyriticus* in the presence of distinct black spots and in the lighter color of the upper parts; from *danielsi* in the lateral concentration of the spots, the absence of a black line along the canthus, and, when large specimens are compared, in the narrower head." Additionally, *duryi* differs from *dunni* by not being profusely flecked dorsally and in lacking the black line along the canthus, and from *palleucus* by undergoing metamorphosis.

Color. A living 89-mm male from Laurel Cave, Carter Co., Ky. (RB 777), anesthetized in chloretone, is described as follows: dorsal ground color a deep maroon-red gradually becoming pinkish-orange on lower sides and ventral surface of tail; large black dots (one per costal groove) along upper sides of body, tail, and head; smaller black dots scattered along lower sides, tail, and side of head; smaller flecks scattered over sides of throat, entire surface of pectoral region, belly, and tail; ventral surface flesh colored, becoming pinkish after anesthetization due to dilation of capillaries; jaws marked by alternating blotches of black and white pigment cells; tiny flecks of white extending from jaws along side of head, lateral body wall, lateral surfaces of limbs, and ventral half of tail; canthus rostralis faintly marked by a thin pigmentless line running from anterior corner of eye to labial end of nasolabial groove; iris iridescent reddish color. An 81-mm specimen from Bat Cave (RB 778) is similar to the above except for a clearer, redder dorsal ground color, absence of ventral dark flecks, and presence of some black dots mid-dorsally.

Status of G. lutescens. Mittleman (1942) stated that *G. p. duryi* probably did not occur at Bat Cave, Carter Co., Ky., even though it is only about three miles from the type-locality. He considered branchiate specimens from Bat Cave (UIMNH 36153–6) to be representatives of a cave-adapted, possibly neotenic, species referable to the description of *Triturus lutescens* Rafinesque, 1832. Two problems posed by his report are: (1) the status of the population of *Gyrinophilus* in Bat Cave, and (2) the applicability of the specific name *lutescens* Rafinesque, 1832, to that population.

Several points in Mittleman's discussion of *G. lutescens* cause question. He indicated that *lutescens* is found "only in the total darkness of the innermost reaches of the cave, in the constantly extremely cold water (4°–6°C.). . . . It seems further probable that this habitat is an undisturbed one with a constant subterranean source of water, with slow seepage as the only means of drainage, for on two occasions, pigmentless and apparently blind fish were noted sharing this habitat." The above description does not fit Bat Cave, Carter Co., Ky., a well-known cave because of large numbers of *Myotis sodalis* which hibernate there. Bat Cave is a tunnel, with water entering below breakdown at one end and exiting as a stream at the other. Refuse from the lodge at Carter Caves State Park is dumped into a gully near the upper entrance of the cave. During heavy summer rains tremendous amounts of water, refuse, and debris are washed into and through the cave. During heavy rains in the summer of 1961, the force of water and debris passing through the cave completely flattened iron gates placed at each entrance. There are no inner reaches to the cave, in the sense of isolated areas not in contact with the outside. Water temperatures in caves of the area of Indiana, Kentucky, and West Virginia are 11–13°C (Davies, 1958; Mammoth Cave National Park records; T. C. Jegla, personal communication). In general, air and water temperatures in the innermost reaches of caves are the same as the mean annual surface temperature of the area. Water temperatures of 4–6°C in Bat Cave could have been recorded only near the upper entrance in winter, where cold surface water enters the cave. There are no reports of blind amblyopsid fish in Kentucky east of the Mammoth Cave region (Woods and Inger, 1957), although several species of stream fish common to the area could have been in the cave. If Mittleman actually was in Bat Cave, Carter Co., Ky., most of the discrepancies between his observations and mine could be explained if he were unaware of the upper entrance and made most of his observations near there in winter.

As judged by personal collections in Bat Cave, the main population of *duryi* seems to be located in the twilight zone and slightly inward from the upper entrance. Adults were found under rocks in pools of water and on wet mud banks at some distance from water. Larvae were most abundant in pools and in the stream itself near the upper entrance, but could be found throughout the cave. Adults and larvae of *Pseudotriton ruber* were also collected in the twilight zone of the upper entrance, and larvae were found throughout the cave. During the summer of 1960, R. Newcomer (1961) collected numerous branchiate salamanders in Bat Cave, but found only larval *duryi* and *P. ruber.* It is apparent that Mittleman applied the name *lutescens* to larval *G. p. duryi.* Specimens collected by Mittleman and identified by him as *lutescens* (UIMNH 36153–6) are referable to *duryi.*

Mittleman was correct in applying the name *lutescens* to the population of *Gyrinophilus* in Bat Cave, because there is no other salamander in Kentucky to which Rafinesque's description, incomplete as it is, applies. The name *duryi* is a junior synonym of *lutescens.* (An application for the suppression under their plenary powers of the specific name *lutescens* Rafinesque, 1832, was submitted to the International Commission on Zoological Nomenclature [Brandon, 1963] to avoid replacing an established name with an older, little used, and poorly characterized one.)

Criteria of intergradation with G. p. porphyriticus. The presence of dark spots on the upper sides, back, and tail (excluding New England and Canadian specimens), indistinct canthus rostralis, clear, pale ground color dorsally, and immaculate belly on specimens over 79-mm long are considered criteria for genetic influence from *p. duryi.* The absence of spots on the sides, back, and tail, distinct canthus rostralis, dark, mottled or reticulated dorsal pattern, and flecked bellies on specimens over 79-mm long are used as criteria for genetic influence from *p. porphyriticus.* An index of hybridization (similar to that used by Anderson, 1949, in plants, and by Sibley, 1950, in birds) was set up, and each individual was scored numerically as follows:

Dorsal dark spots:	absent	1
	present	0
Canthus rostralis:	distinct	1
	faint	0
Dorsal ground color:	mottled or reticulated	1
	clear	0
Ventral melanophores:	present and numerous	1
	absent	0

Additional criteria of intergradation, or further subdivisions of each criterion, would allow a more diagrammatic representation of the genetic mixing of these two subspecies. Unfortunately, there are very few characters amenable to meaningful quantitative expression in salamanders. In Sibley's work with Mexican towhees, it was possible for him to score "pure" members of one taxon as 24, another as 0, with intermediate values representing various degrees of hybridization. In comparison of *G. p. porphyriticus* and *G. p. duryi,* the former is scored as 4, the latter as 0; intergrades as 1, 2, or 3. Some indication of genetic influence from the respective subspecies is thus achieved, but not as much as would be desirable. Any further subdivision of the criteria of intergradation would be very subjective.

The geographical distribution of numerical intergradation values on Fig. 15 shows that the area of intergradation between *p. porphyriticus* and *p. duryi* is much larger than the area occupied by "pure" *p. duryi.* Intergradation between *p. porphyriticus* and *p. duryi* is further complicated by influence from *p. danielsi* and *p. dunni* in the region immediately south of the northern borders of Tennessee and North Carolina and in Alabama, but it is well demonstrated north of these areas. The fine collection of the West Virginia Biological Survey contains many specimens showing diagrammatically the change from *p. duryi* near Huntington, Cabell Co., to *p. porphyriticus* in the mountainous northeastern part of the state.

An interesting aspect of intergrade populations between *p. porphyriticus* and *p. duryi* is seen during the development of the adult pigmentation. Genetic influence from *duryi* shows up most strikingly in newly metamorphosed and young adult specimens. For example, large specimens from Cincinnati (UIMNH 50128, 101 mm; UIMNH 50426, 103 mm) are as darkly mottled dorsally and laterally as any New York specimen examined and have no indication of dark dots on backs or sides. A 63-mm specimen (RB 776) from the same locality looks like *duryi* except for a more distinct canthus. The small specimen has dark dots along the sides and over the back as in *duryi,* and had a clear orange-pink ground color dorsally in life. A specimen from Endless Caverns, Nelson Co., Va. (also within the range of overlap between *p. porphyriticus* and *p. duryi*), mentioned by Dunn (1926, p. 262), was probably similar to RB 776 in coloration. The same ontogenetic trend can be shown with West Virginia and Alabama specimens. There is no reason to regard the early appearance and later disappearance of the *duryi* pattern as indicating an ancestral position for *duryi* (as was suggested by Dunn, 1926, p. 262). The characteristic dorsal dots appear in topotypic *duryi* immediately after metamorphosis, or even on large larvae. The characteristic dark, mottled dorsal pattern of *porphyriticus* develops

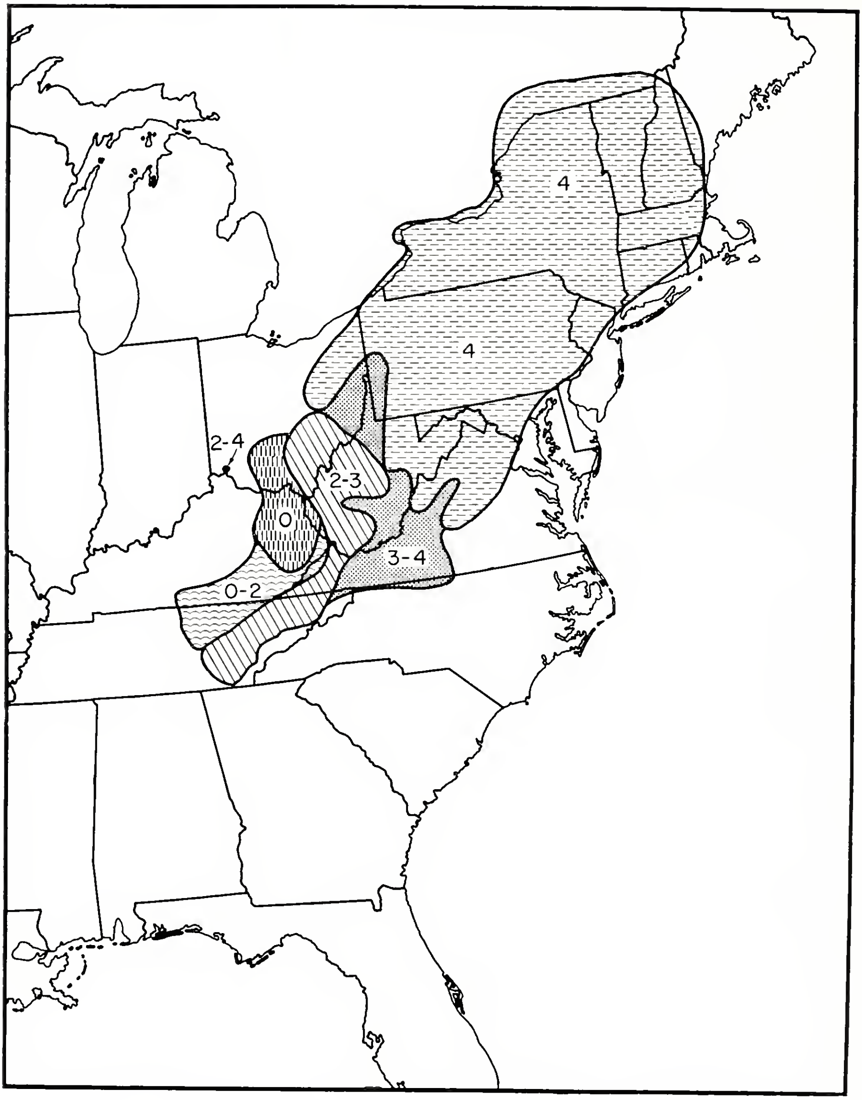

FIG. 15. Geographic distribution of numerical intergradation values between *G. p. porphyriticus* and *G. p. duryi*.

slowly with age. In areas of intergradation, the *duryi* pattern is apparent on newly metamorphosed individuals, but is gradually obliterated by the development of the darker mottlings of *porphyriticus*. On most specimens in areas designated on Fig. 15 as 2–3, the dark dots persist on the sides and tail and remain visible in adults. On some larger specimens from areas designated 3–4, the dark dots persist, but usually they can be seen only on smaller specimens. To be certain of the degree of genetic influence from each of these two subspecies in a given population, individuals of all sizes must be examined.

Specimens examined. Specimens considered to represent "pure" populations of *p. duryi* were examined from the following localities:

KENTUCKY: *Carter Co.:* Bat Cave (OUVC 2547, 2686, 2687, 2688, 3921, 3922, 3923, 3924, 3925; UIMNH 50144; USNM 115521); Carter Caves (CM 17551; CNHM 91276; OUVC 2952, 3012–3; UIMNH 101155; UMMZ 103332); Carter Caves State Park (UK); Cascade Caverns (CNHM 91273–4; MCZ 17540; OUVC 3919–20; UK; UMMZ 109190, 112295); Cascade Caves (CM 10937; UIMNH 36159–60; UK); Cattle Cave, near Carter (UIMNH 50145–6); Laurel Cave (OUVC 2439; RB 777); (OSM 725.1). *Fayette Co.:* 10 miles southeast of Lexington (RN). *Floyd Co.:* (UMMZ 86574–5). *Greenup Co.:* 2.5 miles northeast of Kehoe (CJH 204). *Harlan Co.:* top of Big Black Mountain (UK). *Knott Co.:* between Hindman and Lackey (UIMNH 36161). *Lewis Co.:* Pipe Lick, 1 mile north of route 59 on road to Garrison (WBB); 3 miles southeast of Scott Branch School on route 24 (WBB). *Mason Co.:* near mouth of Cabin Creek (UK); 0.5 mile southwest of Maysville (UK). *Menifee Co.:* 4 miles east of Frenchburg on U.S. route 60, Cumberland National Forest (CJH 138). *Powell Co.:* 2.5 miles east of Nada (UMMZ 116347); 2 miles west of Powell-Wolfe county line (UK).

OHIO: *Adams Co.:* Blue Creek Road, above Puntenneyville, Green Twp. (OSM 179.8, 179.10); Buttermilk Run, Jefferson Twp. (UIMNH 50138–41, 50143); Green Twp. (UMMZ 88852); Mineral Springs (UMMZ 95921–2); Moon Run, Jefferson Twp. (UMMZ 120349); southeast quarter of county (UIMNH 50142). *Highland Co.:* Seven Caves, Paint Twp. (OSM 249.20). *Pike Co.:* Benton Twp., 1 mile north of Morgantown (OUVC 3946); cave near Byington, Mifflin Twp. (OSM 339.9); 2.25 miles west northwest of Byington (UMMZ 111656); Coopersville (CM 5850–51; UMMZ 71786); Kincaid Creek, southeastern Perry Twp. (OUVC 3439); Pike State Park (OUVC 3673); Pike State Park, 0.5 mile west of headquarters (JAM 34.1–.2, 34.9–.18); near Piketon (USNM 118296); Richardson Hollow, northwestern Benton Twp. (OUVC 3438); Star Hollow, near Coopersville (OSM 587.5–.15). *Scioto Co.:* Roosevelt Lake, Shawnee State Forest (OUVC 3085).

WEST VIRGINIA: *Mingo Co.:* 0.25 mile west of Matewan (WVBS 2735, 2737).

VIRGINIA: *Buchanan Co.:* 4 miles from Grundy (USNM 12750–1).

The following specimens are considered to represent intergrade populations between *p. porphyriticus* and *p. duryi:*

KENTUCKY: *Bell Co.:* 3.3 miles north of Middlesboro (UMMZ

113381). *Cumberland Co.:* 4 miles east of Leslie (UK). *Jackson Co.:* 2 miles north of Tyner (UK); (CJH 5). *Monroe Co.:* 1 mile south of Cyclone (UK). *Pike Co.:* near Wales (CM 16340). *Whitley Co.:* Cumberland Falls State Park (KLW 1727–29; UK).

NORTH CAROLINA: *Stokes Co.:* Hanging Rock State Park (OUVC 4192).

OHIO: *Athens Co.:* Stewart (OUVC 2966); Troy Twp. (OSM 65331). *Fairfield Co.:* sect. 24, Madison Twp. (UMMZ 95937). *Hamilton Co.:* Ault Park (RB 776–7); French Park, Amberly Village (JTC 71, 206, 221; RB 602; UIMNH 50129); Indian Hill (JTC 281); Madeira (UIMNH 50130–1, 50135). *Hocking Co.:* sect. 4, Benton Twp. (UMMZ 95940); sect. 30 or 31, Benton Twp. (UMMZ 95941); Cantwell Cliffs State Park (OUVC 3705, 3896; UMMZ 98742); Conkle's Hollow State Park (OUVC 3175; UMMZ 111655); sect. 16, Goodhope Twp. (UMMZ 95938–9); Goodhope Twp. (CNHM 91271; OSM 501.1); sect. 27, Laurel Twp. (OUVC 3871); Little Rocky Branch, Laurel Twp. (CNHM 91269–70); northeastern sect. 32, Marion Twp. (RB 774; UIMNH 50424); Old Man's Cave State Park (UMMZ 111652–3); Rhododendron Hollow, sect. 18, Goodhope Twp. (UMMZ 98741); Salt Creek Twp. (CNHM 91268). *Jefferson Co.:* Amsterdam (UIMNH 36178). *Licking Co.:* Rocky Fork, Eden Twp. (OSM 326.15); Wakatomika Creek, Fallsburg (OSM 834.8). *Monroe Co.:* near Altitude, Adams Twp. (OSM 632.3). *Morgan Co.:* Malta [?] Twp. (OSM 4398.29–.30). *Muskingum Co.:* Otsego (OSM 949); 1 mile north of New Concord (OSM 860). *Ross Co.:* Tar Hollow (UMMZ field ser. 1916). *Washington Co.:* Marietta (UIMNH 50137; USNM 118297); Squaw Hollow, sect. 35, Marietta Twp. (OUVC 2465, 3292).

TENNESSEE: *Bradley Co.:* 4 miles north of Cleveland (RMS 351). *Claiborne Co.:* Harrogate (MCZ 26711). *Clay Co.:* Sheals Cave (TCB). *Cumberland Co.:* Spencers Rock Cave (TCB). *Grainger Co.:* 8 miles east of Blaine (UMMZ 95746). *Green Co.:* Afton Cave (JDL). *Jefferson Co.:* Indian Cave, near Jefferson City (USNM 68162, 68820). *Putnam Co.:* Algood School Cave (TCB). *White Co.:* Rockhouse Cave (TCB); near Rockhouse Cave (RB 766, 781). *Union Co.:* Central Peninsula Wildlife Management Area (RMS 508); Walker's Ford (NCSC); Wolf Cave (TCB).

VIRGINIA: *Carroll Co.:* 4 miles east of Galax (UMMZ 122749, 122752). *Craig Co.:* 4 miles north of Newport, Clover Hollow Cave (CM 22612–13). *Giles Co.:* Mt. Lake (ANSP 24613–4, 24615–6, 24617, 24618–9; CM 13978–80, 17622–24; UFl 9066). *Grayson Co.:* Whitetop Mountain (TCB; UMMZ 120578). *Henry Co.:* Martinsville (Figsboro Road) (UMMZ 122748); Spencer (CM 18103). *Lee Co.:* Lucy Beatty Cave, 3 miles south of Rose Hill (JH). *Montgomery Co.:* Blacksburg

(USNM 143697–8, 143702–4); Old Mill Cave, near Ellett Station, about 3 miles southeast of Blacksburg (GRT 1277). *Pittsylvania Co.:* northwestern Comer, Smith Mountain (DU A614). *Scott Co.:* Horton's Cave, 10 miles southwest of Clinchport, near Tennessee-Virginia line (JH). *Tazewell Co.:* Lawson's Cave, Burkes Garden (USNM 124508); Ward Cove Cave (TCB).

WEST VIRGINIA: *Brooke Co.:* Wellsburg (WVBS 2295). *Cabell Co.:* Huntington (CM 19394, 19400, 19402); Huntington, Enslow Park (WVBS 1350–1); Huntington, Gwinn's Woods (WVBS 1593); Huntington, Lions' Den, Ritter Park (WVBS 1296, 2122); 1 mile south of Huntington (UMMZ 96001–2); 2 miles south of Huntington (CM 18149–50); 4 miles south of Huntington (CM 15844); 1 mile southeast of Huntington, Pleasant Valley (WVBS 1745–6, 2079). *Fayette Co.:* 1.3 miles east of Charlton Heights (WVBS 2642); Fayetteville (WVBS 2603); Kirby Hollow (WVBS 2639–40). *Kanawha Co.:* Belle, near DuPont High School (WVBS 2448); 2 miles east of Charleston (WVBS 2303); Hadley (WVBS 2315, 2648). *Logan Co.:* Chapmansville, on hill behind school (WVBS 2620–5). *Marion Co.:* Fairmont (CNHM 91265). *McDowell Co.:* 1 mile north of Maybeury (RB). *Monroe Co.:* Argobrites Cave (TCB); Fletcher Cave, near Gap Mills (TCB). *Nicholas Co.:* Snake Den Mountain, north of Richwood (WVBS 415). *Ohio Co.:* Oglebay (UK). *Pocahontas Co.:* Marlinton (WVBS 789–90); near Thornwood (WVBS 2060). *Putnam Co.:* Red House, 0.5 miles above ferry landing (WVBS 2641). *Raleigh Co.:* Shady Springs (WVBS 2601). *Randolph Co.:* near Guadineer Knob, northeast of Cheat Bridge (DU A617–18); 6 miles south of Huttonsville, Fall Rock Run (WVBS 780); near Pickens (CNHM 27819). *Summers Co.:* 3 miles west of Hinton (WVBS 2599). *Wayne Co.:* 1 mile south of Buffalo High School (WVBS 2299); Kraut Creek, near Spring Valley Country Club (WVBS 2400–1); 1 mile east of Louisa (CM 18136–7, 18150). *Webster Co.:* Williams River (WVBS 2514); Red Oak Knob (CU 5980). *Wyoming Co.:* Pineville (WVBS 2479).

Status of G. porphyriticus from Tennessee. Tennessee is one of the most complex areas in the range of *Gyrinophilus.* Populations west of the drainage of the Tennessee River and its tributaries, in the drainage of the Cumberland River, are southern extensions of intergradation between *p. porphyriticus* and *p. duryi* (Fig. 21). These populations are quite similar to intergrade populations in West Virginia and are relatively uniform among themselves. *G. p. porphyriticus* extends down the Tennessee River drainage and intergrades with *p. dunni* in northwestern Georgia and in northern Alabama. *G. p. danielsi* occurs in the mountains of Tennessee, along the eastern boundary of the state, and extends to the western border of the mountains. The distribution of the cave-adapted *G. palleucus* is still incompletely known; it has been taken from caves opening on the edges of the southern Cumberland Plateau, and in the Tennessee Valley. The species may also occur in unexposed cave systems and ground water beneath the level of the Sequatchie and Tennessee rivers, from Franklin County to Roane County, at least.

Kentucky distribution. Most previous publications (Bishop, 1943; Walker and Weller, 1932; Mittleman, 1942) extended the range of *p. porphyriticus* into Kentucky south of the northeastern counties, apparently on the basis of one specimen from Estill County (USNM 57357). The specimen was described and correctly identified as *p. porphyriticus* by Walker and Weller (1932) and was identified by Mittleman (1942) as *p. inagnoscus.* The specimen is in fact "typical" of New York *p. porphyriticus;* it is likely that it did not originate in eastern Kentucky but was fortuitously transferred there by unknown persons. All other specimens from Kentucky are either *p. duryi* or intergrades between that and *p. porphyriticus.* Conant (1958, p. 143, map 186) correctly showed *p. duryi* extending throughout eastern Kentucky and into West Virginia and Virginia. His map apparently was based in part on unpublished data.

Seibert and Brandon (1960) recorded a specimen (OUVC 3256) from Pike State Park, Pike Co., Ohio, which was similar to *p. porphyriticus.* The unusual nature of its collection raised some doubt as to its actual site of origin at that time. Since that report was made, much additional material from Pike County has been examined, all of which is representative of *p. duryi.* It now seems improbable that the specimen (OUVC 3256) was actually from a population in Pike County, but could have been carried in from as near there as Cincinnati.

Gyrinophilus porphyriticus dunni Mittleman and Jopson

Gyrinophilus dunni Mittleman and Jopson, 1941 (in part): 1–5, pl. 1.
Gyrinophilus danielsi dunni: Bishop, 1943: 365–367, Fig. 108.

Holotype. Female, USNM 11320, collected 8 April 1941, by A. Grobman.

Type-locality. Campus of Clemson College, Pickens Co., S.C., 700 feet above sea level.

Paratypes. The original description of *dunni* was based on such a hodgepodge of specimens that its limits were for some time misunderstood, and are not yet satisfactorily defined. Reese (1950) pointed out that the two Jefferson Co., Tenn., paratypes are actually *p. porphyriticus.* I examined the two specimens, USNM 68820 and 68168, and agree with his identification. Two other paratypes, USNM 102441 and CHM 28.144.4, are larvae. The identification of larval *Gyrinophilus porphyriticus* has not yet been perfected to the point that they are useful in taxonomic studies, but it is certain that the latter, at least, is a larval *p. dunni, sensu stricto,* because of its collection locality. It is likely that the paratype from "Three Springs, near Russellville, Hawkins County, Tenn., 1,350 feet" was a *p. porphyriticus,* or intergrade between that and *p. duryi.* The specimen could not be located; it was not given a collection number, and neither Mittleman nor Jopson has the specimen now (personal communication). The other paratypes, from Haywood Co. (Bishop collection), Yancey Co. (NCSM 4905), and Jackson-Macon county line (NCSM 7198), N.C., in the light of other specimens from these areas, cannot be considered *p. dunni, sensu stricto.* The Yancey County specimen is identified by me as *p. danielsi,* and the Jackson-Macon specimen as an intergrade between *p. danielsi* and *p. dunni.* I have not examined the Bishop specimen from Haywood County.

It is fortunate that the holotype of *p. dunni* was one of a series of specimens that can be considered characteristic of a distinct subspecies. Of the paratypes listed by Mittleman and Jopson, only those from South Carolina can be considered representative of this subspecies: *Greenville Co.:* Caesars Head, 3000 feet (USNM 102440). *Oconee Co.:* Walhalla, 1000 feet (Clemson College Division of Entomology and Zoology 105). *Pickens Co.:* Clemson College, 700 feet (Clemson College Division of Entomology and Zoology 35, 58; M. B. Mittleman collection 383–4; NCSM 7594); Rocky Bottom, 2000 feet (CHM 35.141.12).

Diagnosis. A metamorphosing *Gyrinophilus* with dorsum of head, back, limbs, and tail profusely flecked with dark pigment (Fig. 1C); flecks becoming abruptly fewer along mid-sides, and often grouped into a chevronate pattern mid-dorsally, especially on larger specimens; lower sides, throat, pectoral region, and belly usually without melanophores, occasionally a few dots on pectoral region and throat of largest individuals; lower jaw marked with alternating patches of black and white pigment; snout broad; canthus rostralis very distinct, consisting of a pigmentless orbitonasal line bordered below by black; differs from *p. porphyriticus* in shape of pre- and paravomerine tooth series, presence of numerous individual flecks on back, sides, etc., and by lack of a dark, mottled dorsal ground color; from *p. danielsi* and *p. duryi* by being profusely flecked dorsally; from high-elevation *p. danielsi* by lacking well-pigmented throat; from *duryi* by the more pronounced canthus rostralis bordered below with black.

Diagnostic value of size. Maximal size was used in the original diagnosis, but was not found to be useful. Statements of maximal size for salamanders based on small samples are, in most cases, probably not even fair estimates of true populational limits. In mammals and birds, which are limited in adult size both hormonally and by loss of epiphyseal plates between a diaphysis and epiphyses in long bones and vertebrae, maximal size can be a very useful taxonomic character. Salamanders, however, are not limited in growth by such structural features. They continue to grow throughout life, although probably at a greatly decreased rate as they age. *G. p. dunni* was characterized as a "considerably smaller" form than *p. danielsi*, presumably on the basis of the small size of the paratypes. Fig. 16, based on the original paratypes of *dunni* and additional specimens collected since 1941, shows that there is no significant difference in length between *p. danielsi* and *p. dunni.*

Color. A 91-mm female (living, anesthetized in chloretone), collected near Blue Ridge, Fannin Co., Ga. (RB 782): innumerable black flecks forming a chevronate pattern dorsally over a reddish-orange ground color; ventral surface pigmentless, flesh colored (appearing pinkish due to dilated capillaries after anesthetization); a patch of white pigment across posterior throat; white pigment very prominent on jaws, covering more area than intervening black blotches; white flecks evident along sides of head, sides of body, tail, and lateral margins of limbs (all white pigment dissolved out after a few hours preservation in alcohol-formol-acetic acid fixative [AFA]); canthus rostralis marked as a narrow, pigmentless band extending from the upper eyelid to the labial end of the nasolabial groove; canthus outlined below by a narrow band of black; iris iridescent reddish color.

Range. Regions of contact between the southern Appalachian Mountains and the Piedmont in northeastern Georgia, northwestern South Carolina, and southwestern North Carolina.

Reese (1950) pointed out that *p. dunni* does not occur northwest of the Great Smoky Mountains National Park, but he extended its range up onto the low elevations of Mt. Mitchell, Yancey Co., N.C., apparently on the basis of Hairston's work there (1949), and the paratype from Cane River (along the northwest side of Mt. Mitchell). In doing so he upheld Mittleman and Jopson's concept of *dunni* in Yancey Co. and Haywood Co., N.C., and in addition, listed records from Buncombe County. Thus, although Reese eliminated the *p. porphyriticus* element from the original description of *p. dunni,* low-elevation *p. danielsi* remained. The record from Buncombe County (CNHM 19234) is actually identifiable as low- or mid-elevation *danielsi.* It is likely that *danielsi* and *dunni* intergrade in southern Haywood County. Two specimens examined from Haywood County (USNM 57120; UIMNH 36158) are *danielsi.*

Reese (1950) extended the range of *dunni* throughout northern Georgia, except the four northwestern counties, but I am unable to determine the basis for the extension. He quoted a record for *danielsi* from Floyd Co., Ga., from ". . . Dunn (1926, p. 271). . . ." Dunn, 1926, p. 271, listed four specimens from "Upper Georgia," USNM 4716–9, but did not mention Floyd County. The only data for these specimens

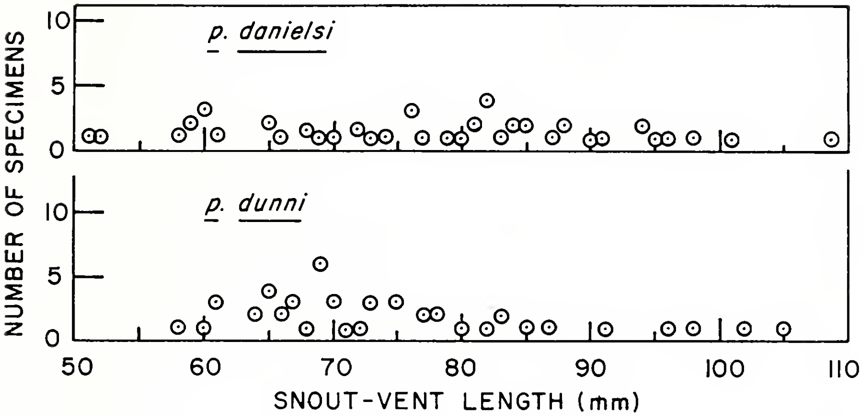

FIG. 16. Size distribution of specimens of *G. p. dunni* and *G. p. danielsi* examined.

in the USNM catalog (Doris Cochran, personal communication) are "Ga." The specimen (only one was borrowed) in question is in bad condition, and no identification was possible. Reese also indicated (on maps) specimens from Murray, Bartow, DeKalb, and Lincoln counties, Ga. I have examined no adult specimen from these counties. Most of these records apparently were taken from the "files of Dr. Bishop," as mentioned by Reese, or from larvae. The Lincoln County record was probably taken from Dunn (1926, p. 271) (ANSP 512). On my invoice ANSP 512 is listed from Lincoln Co., N.C., not Georgia (confirmed in letter from J. Böhlke). Dunn listed the specimen in the wrong state. The specimen (110-mm long), although it is in a poor state of preservation, is similar to specimens from Cabarrus Co., N.C., which are considered to be intergrades between *p. dunni* and *p. porphyriticus.* The snout is broad, but the canthus is not so pronounced as in *p. dunni.* The belly is without pigment. The dorsal pigmentation, as best as can be seen, consists of dark mottling as in *p. porphyriticus.* Individual dots of pigment are evident along the lower sides. The lower jaw is marked with broken blotches of dark pigment as in *p. dunni.*

Dunn (1926, p. 271) listed as questionable the record of *Gyrinophilus* from Columbia, Richland Co., S.C., "USNM 5812." The two specimens in question (actually USNM 8812), 94-mm and 66-mm long, are badly discolored, but are identifiable as *p. porphyriticus.* There is nothing about the specimens to indicate genetic influence from *p. dunni.* In view of the apparent intergradation between *p. dunni* and *p. porphyriticus* in Cabarrus Co., N.C., Clarke Co., Ga., and east-central Alabama, it is possible that the Columbia specimens are actually from there and represent populations of *p. porphyriticus* extending down along the outer Piedmont. It is possible that Dunn did not examine these specimens, since he identified them as *danielsi* (probably by geographical criteria only), and may have questioned the record merely on geographical grounds. Much additional collecting will be necessary to show the status of *Gyrinophilus* there, but it is at least indicative that the southern- and eastern-most populations of *p. dunni* show traits of *p. porphyriticus*.

Specimens examined. The following specimens are identified as *G. p. dunni, sensu stricto:*

GEORGIA: *Fannin Co.:* Blue Ridge (RB 779, 782–3); Mill Creek Fish Hatchery (UG 42); Springer Mountain (UG 435). *Lumpkin Co.:* Winding Stair Gap (UG 328). *Rabun Co.:* Rabun Bald (CM 17792; UG 301, 1043); Warwoman Dell (OUVC 3969–70). *Towns Co.:* Brasstown Bald (UG 568, 938, 969, 1220). *Union Co.:* Tacoa Experiment Station (UG 30). *White Co.:* near Tray Mountain (UG 619); (UG 304).

NORTH CAROLINA: *Cherokee Co.:* 3 miles south of Andrews (HCY); Joanna Bald (UG 1228). *Clay Co.:* Deep Gap (UG 826); Hurricane Creek (BDV 599–604); Licklog Gap (BDV 598). *Henderson Co.:* Argyle Woods (AMNH 21177). *Polk Co.:* 1 mile south of Saluda (RBru M–12); 1.5 miles south of Saluda (RBru S–27); 1.5 miles southeast of Saluda (RBru M–11).

SOUTH CAROLINA: *Greenville Co.:* Caesars Head (USNM 102440); 1.7 miles south of Caesars Head (CHM 49.31.7). *Oconee Co.:* Jocassee (CHM 54.67.21; DU A598–9; UG 652; UMMZ 109179); 0.7 mile south of Jocassee (CHM 54.35.16); 1 mile south of Jocassee (CHM 53.179.22). *Pickens Co.:* Clemson College (CM 21017; NCSM 7594; USNM 113230); 3.5 miles northeast of Jocassee (CHM 54.35.4); 5.6 miles northeast of Jocassee (CHM 54.35.42); 10.9 miles northeast of Jocassee (CHM 54.35.27); 4.9 miles northwest of Jocassee (CHM 54.35.11); 2.3 miles north of Pickens (CHM 54.35.24); 3.6 miles north of Pickens (CHM 54.35.38); 6.4 miles north of Pickens (CHM 54.35.47); 5 miles north, thence 4.4 miles northwest of Pickens (CHM 54.35.32); 5 miles north, thence 5 miles northwest of Pickens (CHM 54.35.6); 5 miles north, thence 6 miles northwest of Pickens (CHM 54.35.8); 1.1 miles by road below summit of Sassafras Mountain (CHM 54.43.6); top of Sassafras Mountain (CHM 52.67.12); junction of routes 288 and 178 (UG 933, 987); (UG 933).

Intergradation with other subspecies. Intergradation between *p. danielsi* and *p. dunni* seems to occur in Graham, Cherokee, Macon, Jackson, Transylvania, and probably Haywood counties, N.C., and in Monroe and Polk counties, Tenn. Additional collecting in other counties along the edge of the mountains and Piedmont may show that *p. dunni* extends farther north along the Piedmont-mountain edge in central-western North Carolina.

The primary observable difference between these two subspecies is in pigmentation. Fairly "pure" *p. danielsi,* both high- and low-elevation populations, have large dark dots, of a variable number, scattered over the head, back, sides, and tail. The intensity of the dark reticulations on the jaws and sides of the head decrease with decrease in elevation in *p. danielsi.*

Individuals of *p. dunni, sensu stricto,* have the back, head, and tail completely covered with tiny, numerous dark flecks, often forming a chevronate pattern dorsally. No large dark dots are present on the back. Only specimens having numerous, tiny dark flecks over the entire dorsal surface (as on the holotype, Mittleman and Jopson, 1942, pl. 1) are considered to be representative of *p. dunni.* The presence of large dots dorsally is considered indicative of intergradation with *p. danielsi.*

The following specimens are considered by me to be representatives of intergrade populations between *p. dunni* and *p. danielsi:*

GEORGIA: *Towns-Rabun county line:* (UIMNH 50151).

NORTH CAROLINA: *Clay-Macon county line:* Standing Indian (CNHM 48041); (TCB). *Graham Co.:* Crest of Snowbirds between Andrews and Robbinsville (CNHM 91143); 17.5 miles east southeast of Tellico Plains, 14.5 miles northwest of Andrews (CNHM 91140–2); near Topton, Talula Creek (BDV 605–6). *Jackson Co.:* Cowee Mountain, 3500 feet (NCSM 7198). *Macon Co.:* Highlands (REG 148, 907, 907.1, 911, 929–31, 934; UG 931; USNM 80419, 80448); near Highlands (UG 931, 995); 2.6 miles southwest of Highlands, road to Horse Cove (CHM 54.67.13); Rattlesnake Spring, Wayah Bald (CHM 53.133.12, 54.67.27; UIMNH 50152); Wayah Bald (DU A600–1; UG 1218); near Wayah Bald (CM 6483); Wayah Gap (CHM 54.67.23; CNHM 91100). *Transylvania Co.:* Blantyre (USNM 38228–30); Pink Beds, Brevard-Maynsville Road (UMMZ 102440); 1 mile east of Pisgah Gate (CNHM 91145); 3 miles west of Toxaway Gorge (NCSC).

Several specimens are considered to be intergrades between *p. dunni* and *p. porphyriticus:*

ALABAMA: *Clay Co.:* east side of Cheaha Mountain (BDV). *St. Clair Co.:* McLendon's Cave (TCB). *Talladega Co.:* 2.5 miles southeast of Munford (BDV).

GEORGIA: *Clarke Co.:* near Athens (UG 285); 2 miles east of Athens (UG 245); 3 miles north of Athens (UG 212); 3 miles north of Athens (UG 511); (UG 552).

NORTH CAROLINA: *Cabarrus Co.:* 5 miles east of Davidson (DC 4711). *Lincoln Co.:* (ANSP 512).

SOUTH CAROLINA: *York Co.:* Kings Mountain National Military Park (DC 5673).

In certain areas the identification of specimens would be expected to be complicated by intergradation among *p. porphyriticus, p. dunni,* and *p. danielsi* (e.g., the area north of the junction of the Tennessee, Georgia, and North Carolina state lines). Intensive field work in individual drainages in this area should provide a basis for a clearer understanding of relationships among these forms.

Gyrinophilus porphyriticus danielsi (Blatchley)

Spelerpes danielsi Blatchley, 1901:760–762.
Gyrinophilus danielsi: Fowler and Dunn, 1917:19.
Gyrinophilus porphyriticus danielsi: Stejneger and Barbour, 1933:15.
Gyrinophilus danielsi X *duryi:* King, 1939:554–6, Fig. 6.
Gyrinophilus dunni Mittleman and Jopson, 1941 (in part):1–5.
Gyrinophilus "X" of Mittleman, 1942:37–38, pl. IV.
Gyrinophilus danielsi danielsi: Bishop, 1943:361–365, Fig. 107.
Gyrinophilus danielsi polystictus Reese, 1950:1–7, Fig. 1A (holotype CNHM 91108, collected on Mt. Mitchell, Yancey Co., N.C., at 6000 feet).

Lectotype. MCZ 6638, a female, one of Blatchley's "cotypes," is hereby designated lectotype. This is the specimen for which measurements were listed by Blatchley (1901, p. 771). The specimen was collected by Mr. L. E. Daniels in the "summer, 1900."

Type-locality. ". . . on the side of Mt. Collins and at Indian Pass, at an altitude of 3,000 to 5,000 feet [Great Smoky Mountains National Park]."

Paralectotype. MCZ 6639; collection data same as for lectotype.

Diagnosis. Blatchley's description compared this form with *Spelerpes ruber* (*Pseudotriton ruber*) and *S. montanus* (*P. montanus*) with which he considered it closely allied, but not with *Gyrinophilus porphyriticus.*

G. p. danielsi (Fig. 1D) is a metamorphosing *Gyrinophilus* differing from *p. porphyriticus* by lacking a dark, mottled or reticulated dorsal pattern and by having large, distinct black dots dorsally, a more pronounced canthus rostralis, and paravomerine teeth not convergent anteriorly; from *p. duryi* by having a more pronounced canthus rostralis, uniformly scattered dorsal dark dots, and paravomerine teeth not convergent anteriorly; from *p. dunni* in having larger and fewer dorsal dots, and, in high-elevation populations, melanophores scattered over the throat.

Walker and Weller (1932) reported that their specimens of *danielsi* could be distinguished from *duryi* by red venters in the former, white venters in the latter. Although I have not seen a red belly on any specimen of *danielsi* collected from elevations below 5240 feet, two specimens, from around 5400 feet and around 6000 feet near Indian Gap, Great Smoky Mountains National Park, had orange-red bellies.

The collection locality was not given for Walker and Weller's specimens. It is possible that populations at the highest elevations have reddish bellies, but this trait is not characteristic of the subspecies.

Description of the lectotype (Blatchley's measurements [1901, p. 761] for the larger of his two specimens follow, in parentheses, my measurements of the same structures on MCZ 6638). Female; 19 trunk vertebrae (18 costal grooves); head width at widest point, 13.4 mm (12.5 mm); snout to posterior angle of vent, 87 mm; snout to anterior angle of vent, 83 mm; snout to gular fold, 18 mm (18 mm); tail length, 55 mm (65 mm); total length, 143 mm (160 mm); length of anterior limbs, 16 mm (17.5 mm); distance from axilla to groin, 47 mm (62 mm); intercostal spaces between appressed limbs, 6.5 (7.25); total number of premaxillary and maxillary teeth, 99; total number of prevomerine and paravomerine teeth, 189; canthus rostralis marked by a pigmentless line extending from upper eyelid onto slight cirral swellings at end of nasolabial groove, and by an irregularly margined black line below; distance between outer margins of pigmentless canthal lines at level of external nares, 6.3 mm; head and back marked with fairly numerous, irregularly shaped black dots, 0.6–1.5 mm in diameter (an average of 13 per intercostal space over the epaxial muscle mass); sides, side of head, and back marked with smaller (0.38–0.87-mm diameter), more numerous dots; dotting extending as far ventrally on sides as mid-limb insertion; ventral surface of tail and belly without dark pigment; dotting on side of head extending onto throat, gular fold, and lateral pectoral region. The body cavity is opened by a cut extending along the right side of the belly and across the belly in front of the pelvic girdle. The ovaries contain ova 0.3–0.4 mm in diameter.

The amount of shrinkage evidenced by most measurements (7.5–9 per cent) is not excessive for a specimen preserved for 62 years. The apparent increase in head width is probably due to a typographical error in the original paper. I see no reason to doubt that MCZ 6638 is a specimen used by Blatchley in his description of *Spelerpes danielsi.*

Variation. The taxonomic literature dealing with *danielsi* and *dunni* is replete with contradictory identifications and theories of relationships between the two forms. The inclusion of low-elevation *danielsi* in the original description of *dunni* caused more misunderstanding than any other one factor. No agreement exists on the extent of variation within the subspecies or on their probable zones of intergradation. Some authors recognized the existence of ontogenetic and altitudinal variation in pigmentary characters, but for lack of suitable material either did not realize its significance or simply ignored it.

The one character used consistently in identifying specimens of *danielsi* was the presence of numerous dots or reticulations of black on the throat. Fig. 17 shows that the amount of ventral pigment present on specimens of *danielsi* from the Great Smoky Mountains National Park increases with an increase in length and with increase in elevation. Nearly all metamorphosed specimens from high elevations (4000–6000 feet) have some black pigment on the throat. Numbers plotted on Fig. 17 were derived by estimating separately the amount of pigment on (1) the throat, (2) pectoral region, and (3) belly: 1 = few dots, 2 = moderate number of dots, and 3 = heavily dotted. The numerical values for each of the three regions were totaled and plotted. For example, elevation, 6000 feet; snout-vent length of specimen, 98 mm; throat, 3; pectoral region, 3; belly, 1; total = 7.

The nature of ontogenetic variation in ventral pigmentation in topotypic *p. danielsi* has not been pointed out previously. On 19 specimens collected between Newfound Gap and Clingmans Dome, Great Smoky Mountains National Park, the amount of ventral pigment varied directly with specimen length. These specimens ranged from 52 to 98 mm in snout-vent length. The development of pigment always proceeded posteriorly. If the belly was pigmented, the pectoral region and throat were also well pigmented. If the pectoral region was pigmented, so was the throat. The throat was sometimes the only part of the ventral surface with pigment.

Specimens from high elevations on Mt. Le Conte, larger specimens from near Clingmans Dome, Peck's Corner, Laurel Top Mountain, and Mt. Chapman, Great Smoky Mountains National Park, identical to the description of *polystictus*, were examined (Fig. 17). None of the diagnostic characters for *polystictus* (Reese, 1950) will separate larger high-elevation *danielsi* in the Great Smoky Mountains National Park from specimens of equal size from Mt. Mitchell and Balsam Gap. To continue the recognition of *polystictus*, one would have to recognize colonies of this subspecies atop the higher mountains of the southern Appalachians, each isolated from the rest and continuous with populations of *danielsi* at lower elevations. There is no reason to think that populations of *polystictus* do not merely represent the upper end of an altitudinal cline of ventral pigmentation in *danielsi*. It is apparent that ventral pigment is characteristic of all high-altitude *danielsi*, although its extent and intensity vary ontogenetically. Strangely enough, Reese (1950, p. 4) noted that at lower elevations the amount of ventral pigment decreased directly with a decrease in elevation. No specimen collected below 3500 feet had more than a few dots of ventral pigment (on the throat). Smaller specimens from intermediate elevations (3500–5000 feet) have little ventral pigment, while larger ones have as much pigment as medium-sized specimens from higher elevations (Fig. 17).

King (1939) identified low-elevation specimens from Tuckaleechee

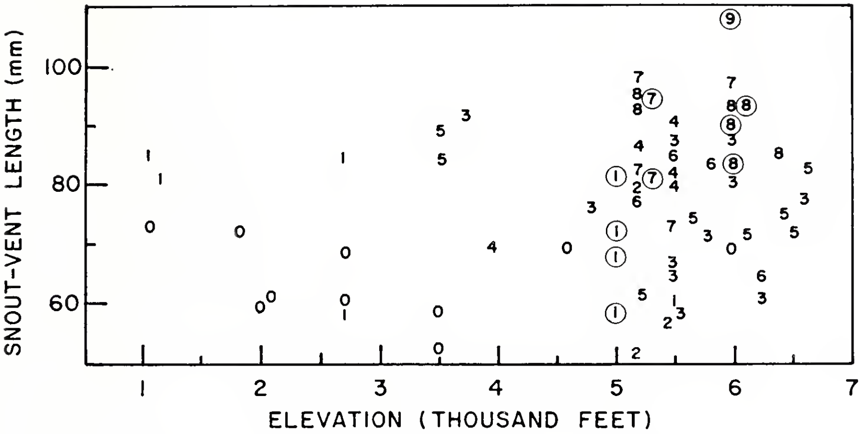

FIG. 17. Amount of ventral pigment in *G. p. danielsi.* The higher the number, the greater the amount of pigment. Encircled numbers are specimens from Yancey Co., N.C., previously identified as *polystictus;* other specimens are from the Great Smoky Mountains National Park.

Cove (1200 feet) and Little River (1100 and 2100 feet), Great Smoky Mountains National Park, as intergrades between *danielsi* and *duryi,* primarily because of their lack of ventral pigment, and a less distinct canthus rostralis. Later, Mittleman (1942) identified the same specimens as *dunni.* Reese (1950) was of the opinion that these specimens actually represented low-elevation *danielsi* and I agree. Four specimens from Tuckaleechee Caverns (NCSC; TCB), 73, 86, 74, and 85 mm long, have little or no pigment ventrally, but dorsally do not differ from high-elevation populations, except for the slightly less distinct canthus. It seems inadvisable to use observed differences between high- and low-elevation populations as the basis for subspecific recognition, since the change appears to be gradual and no zone of abrupt change in characteristics has been shown.

One report (Hairston, 1949) indicated that there might be an ecological and altitudinal break between high- and low-elevation *danielsi.* That report noted that *danielsi* (high elevation) is restricted to spruce-fir forests, *dunni* (actually low-elevation *danielsi*) to hardwood deciduous forests. It is possible that this ecological difference may in part have been responsible for the observed cline in pigmentation, distinctness of the canthus, and pronounced labial reticulations. "Typical" specimens of high-elevation *danielsi,* however, have been collected at Gregory Bald, Jenkins Trail Ridge, and Silers Bald, Great Smoky Mountains National Park, all south of the present limit of spruce-fir forests. Furthermore, since the criteria used by Hairston in identifying his specimens were not recorded (and the description of *dunni* is of no help because of its inclusion of other forms) and since a specimen identified by Hairston as *dunni* was subsequently used as a paratype of *polystictus,* any results of ecological relationships among Hairston's specimens must be re-evaluated after careful examination of his 14 specimens (Hairston, 1949, p. 56), which unfortunately could not be located.

Reese characterized *polystictus* as reaching a larger adult size than *danielsi.* Hairston (1949) also noted that high-elevation *danielsi* were larger. The average total length of the types of *polystictus* was 182 mm (Reese, 1950) (100-mm snout-vent length, judging from the usual percentage of total length taken up by the tail—45 per cent). The largest specimen available to him was probably 112-mm snout-vent using the same estimate. The holotype (CNHM 91108) had a snout-vent length of 111 mm when examined by Reese; 95 mm now. Part of the discrepancy may result from different methods of taking the measurement, part from shrinkage. At any rate, the length of 95 mm is comparable with measurements from other specimens preserved for long periods of time. Fig. 16 shows that these lengths are at the upper end of the length range of *p. danielsi* and *p. dunni.*

It is not difficult to see how Reese received the impression of a large subspecies. On page 1 of his article, he noted that he checked through the Bishop, CNHM, and GSMNP collections (17 specimens, ranging from 120–204-mm total length) for specimens agreeing with the photograph of a large Bishop specimen (1943, p. 363). Since only the large, high-elevation specimens are similar to those of the photograph, Reese unknowingly selected the largest specimens from the collections. The largest specimens available at that time were all collected by Bishop near the summit of Mt. Mitchell (Bishop, 1924).

Most previous investigators regarded low-elevation populations of *Gyrinophilus* in the Great Smoky Mountains National Park and north to Grandfather Mountain, Caldwell, Watauga, and Avery counties, N.C., to be taxonomically the same as low-elevation populations south of the Great Smoky Mountains National Park, or *dunni.* Reese recognized that low-elevation specimens from northwest of the park were not *dunni,* but still considered those from south and east of the park to be of that form. Data presented in the section dealing with *dunni* show that it probably does not extend very far north into North Carolina, and that populations at low elevations east and south of the park are low-elevation *danielsi* or intergrades between *p. danielsi* and *p. dunni.* It is possible that *dunni* may be shown to extend farther north into central North Carolina along the Piedmont and intergrade with *danielsi* there.

Specimens examined. The following specimens are identified as *p. danielsi:*

GREAT SMOKY MOUNTAINS NATIONAL PARK: along ridge to Alum Cave (UMMZ 100239); within 0.5 mile of Appalachian Trail on

Mt. Collins (RB); between Appalachian Trail and Sweet Ridge (UMMZ 122754); Boulevard Trail (REG 904); stream near Bullhead Mountain (UMMZ 122763); east of Camel Hump Knob, Appalachian Trail (UMMZ 122756); spring above Cherokee Orchard (UMMZ 122760); Chilhowee (AMNH 54160); Chimney Camp Ground (GSMNP Gd–17); Clingmans Dome (MCZ 15871); trail from Clingmans Dome to Andrews Bald (UMMZ 122758); Cross Mountain Road, Tenn. (GSMNP Gd–21, 22, 23, 24, 25, 26); Double Spring Gap, between Clingmans Dome and Silers Bald (UMMZ 83249); up road from Grassy Patch (CM 6527); Great Smoky Mountains (CM 10975); Greenbrier Cove (CAS 530–6, 955, 9260); Gregory Bald (GSMNP Gd–12, 13); Haw Gap, Jenkins Trail Ridge (GSMNP Gd–9); Indian Gap (AMNH 54087; ANSP 26673; CM 35980; GSMNP Gd–11; MCZ 6638–9; UFl 1582, 8096; UIMNH 11872; UMMZ 122757, 122759); Indian Gap Trail (UMMZ 95391); trail between Indian Gap and Clingmans Dome (UMMZ 95392–3); Laurel Fork, near Crib Gap (CM 26937); Laurel Top Mountain (GSMNP Gd–1, 2); Little Indian Gap (UMMZ 111650–1); tributary right fork of Little Pigeon River, near Greenbrier (CNHM 15751, 15754); Little River (GSMNP GdXd–1–2); Loggy Ridge and Fish Prong of Little River (UMMZ 122761–2); Mt. Chapman (GSMNP Gd–15, 16); Mt. Guyot (UMMZ 110200); Mt. Kephart (UMMZ 111648); Mt. Le Conte (AMNH 34586–7; CNHM 91098–9; GSMNP Gd–3, 4, 5, 14, 27, 28; UMMZ 111649); just below Newfound Gap (UMMZ 82777); road from Newfound Gap to Clingmans Dome (TU 17695); Old Trail to Chimneys (GSMNP Gd–6); Peck's Corner (GSMNP Gd–7, 8; UMMZ 110198–9); Ramsey Cascade (UMMZ 88860); Ramsey Prong (GSMNP Gd–19; UIMNH 11871); Silers Bald (GSMNP Gd–20); Sugartree Lick, Cataloochee Divide (GSMNP Gd–10); trail between Sweet Ridge and Sugarland Mountain (UMMZ 122753); Tricorner Knob (GSMNP Gd–18); Webb Overlook on Clingmans Dome Highway (RB).

NORTH CAROLINA: *Avery Co.:* Grandfather Mountain (CNHM 91114; NCSC; UMMZ 75537); Linville (CM 6336–7). *Buncombe Co.:* Balsam Gap (TCB); Balsam Gap, Blue Ridge Parkway, Yancey county line (UFl 8375–1, 2). *Burke Co.:* Linville Falls (DU A609–13, 622–4); Neal Creek (DU A608). *Caldwell Co.:* Grandfather Mountain, 5 miles east of Linville (CM 15830–1). *Cherokee Co.:* 12.5 miles west of Andrews (CNHM 91138–9); Big Haw Knob (UIMNH 50153). *Haywood Co.:* Loco Gap (MCZ 24162–3); Nellie (NCSM 320; UIMNH 36158; USNM 57120); Sunburst (MCZ 2890, 13880). *Watauga Co.:* Boone Fork on Yanahlossee Road (CM 6321). *Yancey Co.:* Balsam Gap (UFl 8375–1, 2; UMMZ 75536, 99606); Blackstone Knob Mountain (MCZ 28286); Cane River (NCSM 4905); Mt. Mitchell (AMNH 22544–5; NCSM 7249–50; UMMZ 75539, 97374). *Uncertain locality:*

Elk Creek (CNHM 91113); Frying Pan Gap, near Big Pisgah (CNHM 91115); between Graybeard and Bald Knob (UMMZ 88889); Horse Creek Bottoms (CNHM 91112); Pisgah Forest (UMMZ 52531).

TENNESSEE: *Blount Co.:* Smoky Cavern (NCSC); Tuckaleechee Caverns (TCB). *Monroe Co.:* Star Mountain, McMinn county line (UIMNH 50148).

The general area of extreme northeastern Tennessee and northwestern North Carolina contains populations that will prove to be significant in showing more clearly the relationships among *p. porphyriticus, p. duryi,* and *p. danielsi.* At present, however, there are few specimens in collections from the area.

The following are considered to be intergrades among *p. porphyriticus, p. duryi,* and *p. danielsi:*

NORTH CAROLINA: *Alleghany Co.:* Baileywick, 7 miles east of Sparta on route 18 at Little River (DU A606); along Brush Creek, 3 miles west of Roaring Gap (DU A607); Roaring River Fish Hatchery (DU A605).

Three specimens, ANSP 4353, 10566–7, Roan Mountain, Mitchell Co., N.C., show characteristics of *p. porphyriticus* and *p. danielsi.*

GYRINOPHILUS PALLEUCUS MC CRADY

Gyrinophilus palleucus McCrady, 1954:200–206.
Pseudotriton palleucus: Blair, 1961:499.

Content. Three subspecies are recognized: *G. p. palleucus, p. necturoides,* and *p. gulolineatus.*

Diagnosis. This rather stout-bodied, neotenic species is similar in body form to larval *G. porphyriticus* (Fig. 18). It differs from the latter by having smaller eyes (see key to species), an increased number of premaxillary, prevomerine, and ptergyoid teeth (averages of 25, 32, 20 and 16, 26, 14 in *palleucus* and *porphyriticus,* respectively), a wider head, and a distinctly spatulate snout.

The reported difference from *porphyriticus* in number of costal grooves (McCrady, 1954) resulted from different methods used in counting them (Lazell and Brandon, 1962). Actually the range in number of costal grooves and trunk vertebrae is the same in *palleucus* as in *porphyriticus* (17–19 costal grooves, 18–20 trunk vertebrae).

Size of eye. Although there is some variation in relative eye size in larval *G. porphyriticus,* in no population is the eye as small as in *palleucus* (Fig. 19). The smallest relative eye size in *porphyriticus* (in *p. dunni*) is still much larger than in *palleucus* of the same body length. An increase in length of the snout and the ratio used in determining relative eye size could give the impression of a smaller eye, even when they are of the same absolute diameter. However, the absolute diam-

FIG. 18. Adult *Gyrinophilus palleucus* (136-mm snout-vent), from Berry Cave, Roane Co., Tenn.

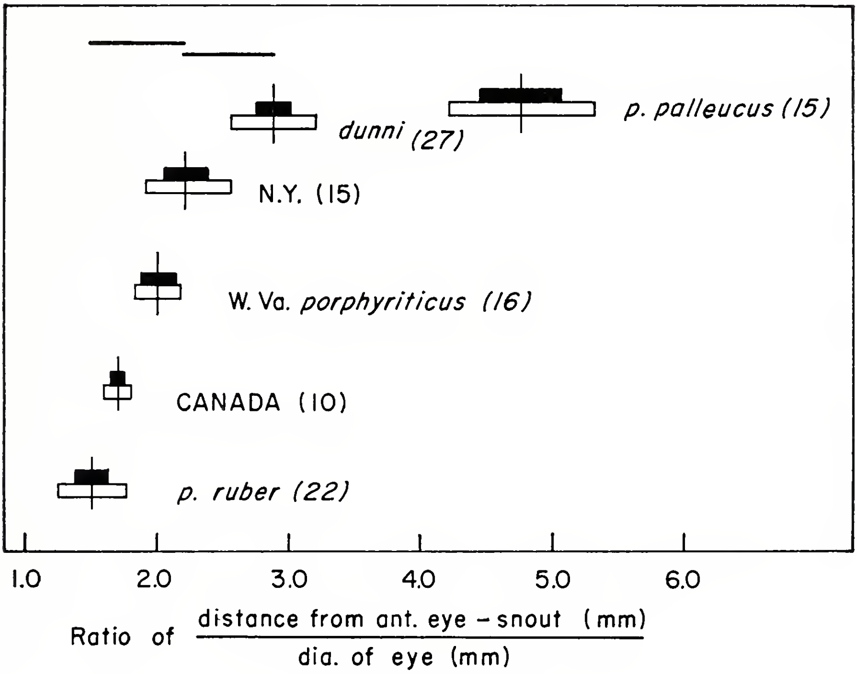

FIG. 19. Relative eye size in *G. porphyriticus*, *G. palleucus*, and *Pseudotriton ruber*. Data shown are means (vertical lines), one standard deviation (white bars), and two standard errors of the mean (black bars). Horizontal lines across the top connect means of samples that are not significantly different (DMRT, $\alpha = 0.05$, $s = 1.083$). Sample size is in parentheses following locality.

eter of the eye increases with a decrease in relative size in the forms examined.

Sketches in Fig. 20 illustrate the difference in snout profile in *p.*

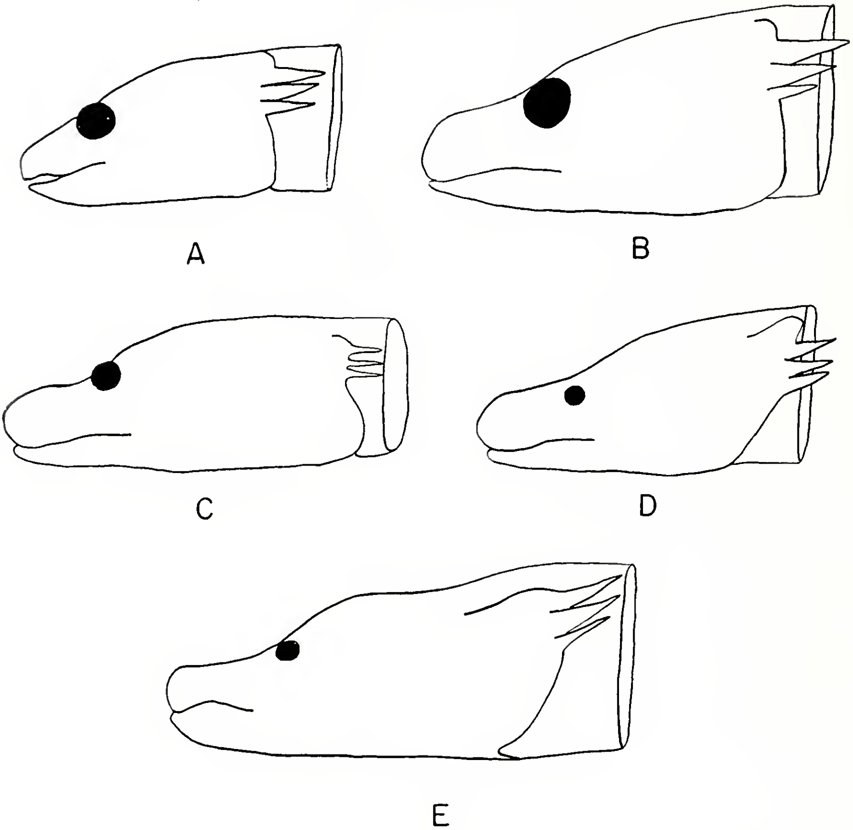

FIG. 20. Freehand profile outlines of heads of: A. *Pseudotriton ruber* (Mammoth Cave National Park, 36 mm); B. *Gyrinophilus porphyriticus* (Cincinnati, Ohio, 57 mm); C. *Typhlotriton spelaeus* (Shannon Co., Mo., 42 mm); D. *G. p. dunni* (Lumpkin Co., Ga., 50 mm); E. *G. p. palleucus* (Franklin Co., Tenn., 73 mm).

porphyriticus, *p. dunni*, and *palleucus* and show a trend toward more spatulate snouts and smaller eyes through the series. *Typhlotriton spelaeus* and *Pseudotriton ruber* are included by way of comparison, the former because it is a cave-adapted species, the latter because it is a member of a closely related genus. Broader, flatter, more spatulate heads are characteristic of the more specialized cave-adapted plethodontid salamanders (e.g., *Typhlomolge* and *Typhlotriton*).

Feeding behavior. The feeding behavior in the laboratory of specimens collected in Custard Hollow Cave, Franklin Co., Tenn., is different from that noted by Lazell (Lazell and Brandon, 1962). Lazell's specimens were kept at room temperature in the light; those from Custard

Hollow Cave were kept in the dark at 16–17°C. Nearly all the specimens ate small pieces of earthworms after being placed in finger bowls in dechlorinated tap water. When a piece of food dropped from a height of a few inches hit the surface of the water near a specimen's head, it was immediately sucked into the mouth, often too quickly to be observed. Large pieces of earthworm, comparable in size to those fed larvae of *G. porphyriticus*, were swallowed by specimens of *palleucus*, but were usually regurgitated a few hours later. Smaller pieces were retained; this may indicate a difference in feeding habits in natural conditions. *G. porphyriticus* feeds on any animal it can swallow, often salamanders over half as long as it is (Bishop, 1941; personal observations); *palleucus* probably subsists on small cave-dwelling invertebrates.

Metamorphosed G. palleucus. Some indication of the neotenic nature of *palleucus* was given by Lazell and Brandon (1962) when they reported a male whose cloaca contained a spermatophore. Dent and Kirby-Smith (1963) reported spermatozoa in sections of testes.

Metamorphic changes can be more easily induced in *G. palleucus* than in any other cave-adapted neotenic salamander. Dent and Kirby-Smith (1963) reported in detail the structural changes induced consistently by thyroxin treatment. Characteristics of their treated specimens (and others reported previously by Dent *et al.*, 1955; Lazell and Brandon, 1962) are compared with those of untreated *G. palleucus*, and with the closely related *Gyrinophilus porphyriticus* and *Pseudotriton ruber* (Table I). The premaxilla notably retains its larval character as a single element. The integument of the anterior part of the head is probably not completely responsive to thyroxin (nasolabial groove remains faint, and no canthus rostralis forms). The peculiar appearance of the head of metamorphosed *G. palleucus* is the result primarily of incomplete metamorphosis in comparison with the closely related *G. porphyriticus*. Certain tissues are responsive to thyroxin (primordial nasal and prefrontal bones, the tongue, gills, tail fin, and parts of the integument), while others are not (premaxilla and part of the head integument). A detailed comparison of treated and untreated *G. palleucus* with *G. porphyriticus* would certainly show other effects of treatment.

Remarks. Although *G. palleucus* has not been reported from any of the caves of Lookout Mountain, two early reports (previously assumed to be of *G. porphyriticus*) may very likely have referred to individuals of this form. Commenting on his visit to Lookout Cave, Hay (1903) noted, "In one deep hole, however, I saw a very pale-colored salamander about 15 cm. in length. It may have been a larval form of some out-of-door species, but it looked quite unlike any with which I am familiar. It swam away with such rapidity when I attempted to secure it that it

TABLE I

COMPARISON OF CERTAIN STRUCTURES IN LARVAE AND ADULTS OF *GYRINOPHILUS PALLEUCUS, G. PORPHYRITICUS,* AND *PSEUDOTRITON RUBER.*

	G. palleucus	Metamorphosed[a] *G. palleucus*	Larval *P. ruber* and *G. porphyriticus*	Adult *G. porphyriticus*	Adult *P. ruber*
Premaxilla	single	single	single	nearly always double	single
Nasal process of premaxilla	separate	separate	separate[b] fused[c]	separate	fused
Nasolabial groove	none	faintly present	none	present	present
Canthus rostralis	none	none	none	present	none
Nasal bones	none	widely separated	none	widely separated	in contact or nearly so
Prefrontal bones	none	not bordering nares	none	not bordering nares	extending from orbit to nares
Eyelids	none	present	none	present	present
Tongue boletoid	no	yes	no	yes	yes

[a] Metamorphosis in this neotenic species must be experimentally induced.
[b] In *G. porphyriticus.*
[c] In *P. ruber.*

soon disappeared in the muddy water." Zipperlen's note (1884) on a specimen found in a cave in Lookout Mountain mentioned the small size of the eyes: "Die Augen sind ausserordentlich klein und liegen sehr weit nach vorne gegen die Mundöffnung zu."

Gyrinophilus palleucus palleucus McCrady

Gyrinophilus palleucus McCrady, 1954:200–206.
Pseudotriton palleucus: Blair, 1961:499.
Gyrinophilus palleucus palleucus: Lazell and Brandon, 1962:300–306.

Holotype. CNHM 72585, female, collected by E. McCrady, January 1944.

Type-locality. Sinking Cove Cave, Franklin Co., Tenn., 5 miles west of Sherwood, at 900-feet elevation.

Paratypes. Although the species was first described on the basis of seven specimens (McCrady, 1954, p. 202), apparently only the holotype was accorded a museum acquisition number and paratypes were not so distinguished. According to Lazell (personal communication), the other six specimens were accidentally desiccated, and the cleared and stained heads are now uncataloged in the Museum of Comparative Zoology.

Diagnosis. This subspecies differs most noticeably from *p. necturoides* and *p. gulolineatus* in its pale body pigmentation in contrast to which the other two subspecies have a dark, spotted dorsal pigmentation.

Range, localities, and specimens examined. G. p. palleucus has been collected from the following caves along the southeastern edge of the Cumberland Plateau.

TENNESSEE: *Franklin Co.:* Cave Cove Cave (McCrady, 1954); Custard Hollow Cave (MCZ 28594; RB 686–9, 768, 773, 780, 789); Lost Cove Cave (McCrady, 1954; MCZ 31880; RB 767); Salt River Cave (McCrady, 1954); Sinking Cove Cave (McCrady, 1954; UFl 7001–1,2,3).

Remarks. At the time *G. palleucus* was described, only 31 specimens had been collected (McCrady, 1954) from five caves over a ten-year period. Dent and Kirby-Smith (1963) collected 41 specimens from the type-locality over a three-year period. On 14–15 November 1961, T. C. Jegla and I found an unusually large population (approximately 60 individuals) of juvenile *G. palleucus* in Custard Hollow Cave, Franklin Co., Tenn. The southern-most entrance of this cave is only 1.5 miles from the south entrance of Sinking Cove Cave, the type-locality. The cave had been examined previously, but large numbers of specimens were not reported nor have so many been seen since. About 20 specimens were taken to the laboratory for experimentation. The specimens range from 37–73-mm snout-vent length and differ in no way from topotypic specimens, with which they were probably continuous geographically and reproductively through ground water connections between the two caves.

Gyrinophilus palleucus necturoides Lazell and Brandon

Gyrinophilus palleucus necturoides Lazell and Brandon, 1962:300–306.

Holotype. MCZ 34100, female, collected by J. D. Lazell, Jr., 29 April 1961.

Type-locality. Big Mouth Cave, near Pelham, Grundy Co., Tenn.

Paratypes. MCZ 34101–4; CNHM 121930, all collected at the type-locality.

Diagnosis. The original diagnosis distinguishes this form as follows: "A neotenic plethodontid salamander with four toes on the forefeet, five on the hind; 21–29 premaxillary teeth in a single uninterrupted series; 15–18 prevomerine teeth on each side; 7–12 pterygoid teeth on each side; 18–19 costal grooves (19–20 trunk vertebrae), 7–8 between appressed toes; dark and heavily spotted dorsally." The body of *G. p.*

palleucus is pale and unspotted. *G. p. gulolineatus* has fewer trunk vertebrae and a dark stripe on the throat.

Variation. The pigmentary variation of living specimens was noted by Lazell and Brandon: "The dorsal ground color varied from russet-brown to a deep brownish-purple. In some specimens (e.g., MCZ 34102), the blackish spots took on a polka-dot like appearance, and were bold and numerous; in others (e.g., MCZ 34103), the spots were fewer in number, and a dark chevronate pattern appeared as well. Small specimens, up to about 120 mm. total length, were as dark as adults, but lacked well defined spotting. All specimens examined had the pale cheek stripe, and even after preservation in alcohol continued to show the double row of light lateral dots."

Range. G. p. necturoides has been collected only from the type-locality.

Intergradation with p. palleucus. Intergrades between *p. palleucus* and *p. necturoides* were reported from Blowing Cave, Jackson Co., Ala., by Lazell and Brandon (1962). Additional specimens from Jesse Elliott Cave and Saltpeter Cave, Jackson Co., Ala., are also considered intergrades. Five of six specimens from the latter cave, 76–91-mm snout-vent length, have a uniformly dark pigmentation dorsally; one specimen has dark *necturoides*-like spots, as do the Blowing Cave specimens. The Blowing Cave and Saltpeter Cave specimens also have an intermediate number of trunk vertebrae, and their eyes are nearer *p. palleucus* in size. The Blowing Cave specimens were incorrectly plotted by Lazell and Brandon from the wrong one of more than three "Blowing caves" in Jackson Co., Ala. Saltpeter Cave and the correct Blowing Cave are the upper and lower entrances respectively of a cave system in the base of Cave Mountain on the edge of North Sauty Creek (part of Guntersville Reservoir).

A few juvenile specimens, unidentified to subspecies, are known from McFarland's Cave and Lim Rock Blowing Cave, Jackson Co., Ala.

Gyrinophilus palleucus gulolineatus Brandon

Gyrinophilus palleucus gulolineatus Brandon, 1965(3):346–352.

Holotype. CNHM 142327, female, collected by R. A. Brandon and J. E. Huheey, 10 July 1963.

Type-locality. Berry Cave, Roane Co., Tenn.

Paratypes. MCZ 44030–32, RB 913, UIMNH 56265–6, collected at the type-locality; and CNHM 142459–61 collected at Athens, McMinn Co., Tenn.

Diagnosis. According to the original description, this subspecies differs from "*p. palleucus* by being more heavily pigmented and having generally fewer trunk vertebrae (18 in 80% of *p. gulolineatus*, in 52% of *p. palleucus*); from *p. necturoides* in vertebral number (no specimen of *p. necturoides* observed has 18); from both *p. palleucus* and *p. necturoides* by having a distinctive dark stripe on the anterior half of the throat, by having a wider head and more spatulate snout, and perhaps by attaining a greater adult size."

Range. Seven specimens have been collected at Berry Cave, and the type-locality, three more from one locality in McMinn Co., Tenn. R. M. Johnson (1958) reported collecting the three McMinn County specimens in 1953 in a roadside ditch at Athens, Tenn. It was Johnson's speculation that the specimens had emerged from a hole in the ground when the ditch was flooded.

There are no known intergrade specimens between *p. gulolineatus* and the other subspecies; it is treated as a subspecies because of its similarity to specimens of *G. palleucus.*

This form will probably be collected in other caves in the Ridge and Valley Province of eastern Tennessee.

Remarks. A notable feature of *p. gulolineatus* is the large size it attains. The largest reported specimen of *p. palleucus* was 101-mm snout-vent (Dent and Kirby-Smith, 1963); the largest *p. necturoides* was 105 mm (Lazell and Brandon, 1962). Of the ten specimens of *p. gulolineatus,* five exceed 100 mm and the largest is 136-mm snout-vent.

ZOOGEOGRAPHICAL CONSIDERATIONS

The complex relationships among the ranges of *G. p. porphyriticus, p. duryi,* and *p. dunni* (Fig. 23) require some attempt at zoogeographical interpretation, even though data from some significant areas are lacking.

Present distribution of the subspecies of *G. porphyriticus* was certainly largely determined by climatic events during and after southward extensions of polar ice during the Pleistocene (see Smith, 1957).

The distribution of the subspecies prior to the glacial advances can only be surmised from what is now known of their distribution and probable genetic relationships, since there is no fossil record.

It is probable that no population remained north of the southern-most edge of Wisconsin glaciation (Fig. 21) during the Pleistocene. Canada, New England, New York, and parts of Pennsylvania, New Jersey, and Ohio were certainly unsuitable when covered with ice. However, it is likely that populations could exist fairly close to glacial borders or in isolated, ice-free islands, since these salamanders are found in cold springs and remain active all winter in waters of near-freezing temperatures.

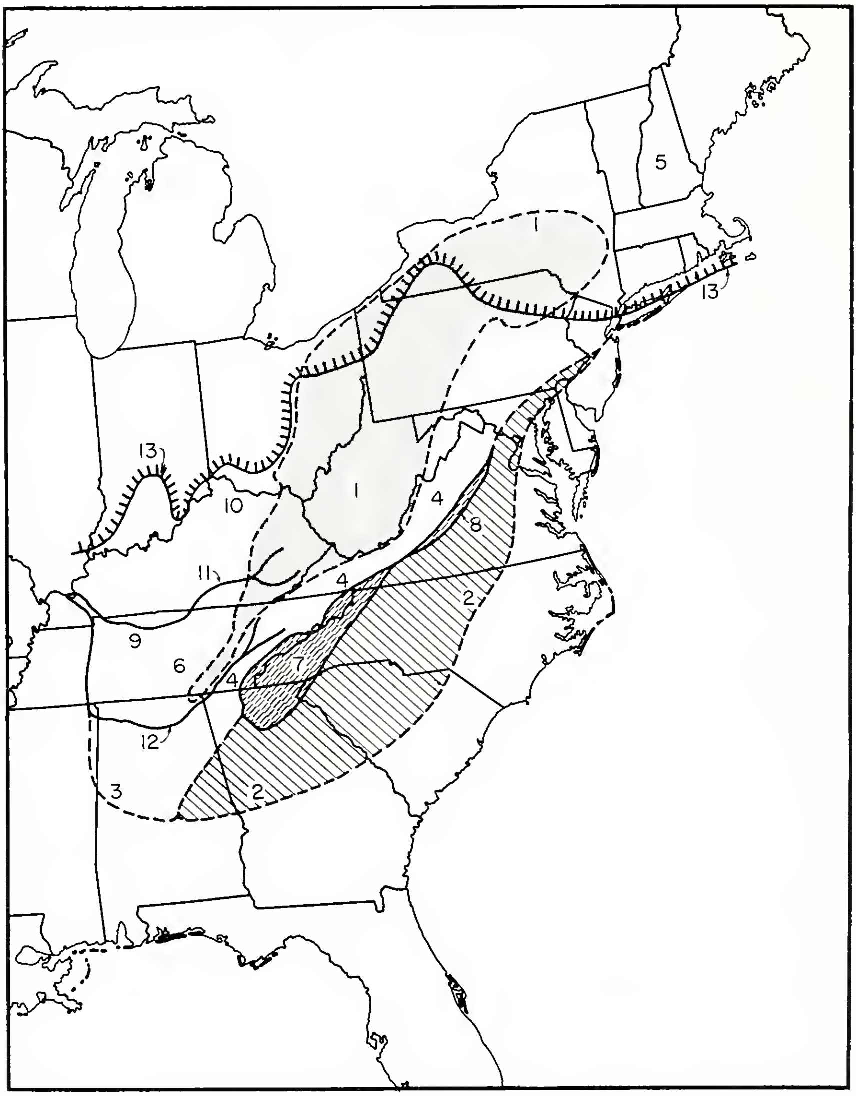

FIG. 21. Major physiographic features of eastern United States associated with the range of *Gyrinophilus*. Appalachian Plateau (1); Piedmont (2); Fall Line Hills (3); New England Province (5); Eastern Highland Rim (6); Southern Appalachian Mountains (7); Blue Ridge (8); Nashville Basin (9); Blue Grass region (10); Cumberland River (11); Tennessee River (12); Wisconsin glacial boundary (13).

It seems certain that Wisconsin-age populations in the northeastern United States and Canada were gradually displaced to the south as advancing ice completely covered their former range. The presence of *p. porphyriticus*-like populations in northeastern Georgia, northern Alabama, and northwestern Mississippi can be accounted for by an extension of *p. porphyriticus* into those areas via the Great Appalachian Valley (Figs. 21–22) during the Pleistocene. In Tennessee, populations on the Eastern Highland Rim, in the Cumberland River drainage, are closer to *p. duryi*, while those in the Tennessee River drainage are closer to *p. porphyriticus* (Fig. 22). It is clear that the *p. duryi*-like populations are most similar to those in southern Kentucky and represent dispersal of Kentucky populations southwestward along the Cumberland River drainage into Tennessee. The populations in the Tennessee River drainage seem to represent a southward movement of *p. porphyriticus* which was influenced genetically by *p. duryi* either before the southward movement, or afterward, or possibly at both times.

It seems likely that at the time of the southern-most extension of glaciation, the three subspecies, *p. porphyriticus* (in Alabama, northeastern Mississippi, northwest Georgia, the Tennessee River Valley, and northward), *p. duryi* (in northeastern Kentucky), and *p. dunni* (in the southeastern Piedmont-mountain border), were fairly well isolated from one another. With the retreat of the glaciers, isolation (in whatever form it might have been) broke down completely between *p. duryi* and *p. porphyriticus* and partially between *p. porphyriticus* and *p. dunni. G. p. duryi,* judging by its huge zone of intergradation with *p. porphyriticus,* is now being assimilated by, or is fusing with, the latter, or at least was doing so prior to the advent of settlers and clearing of forests, pollution of streams, etc. A suggested physical isolating barrier between preglacial *p. duryi* and *p. porphyriticus* is the Teays River, which had its headwaters in the Appalachian Mountains, and flowed northward through the present Scioto River Valley in Ohio (Coffey, 1961). No record exists for *p. duryi* east of the Scioto River in Ohio, but intergrades between it and *p. porphyriticus* occur in southeastern and eastern Ohio. The occurrence of present-day *p. duryi* both south and north of the Ohio River suggests that this form was established in that area before glaciation. The Ohio River seems to have been an effective barrier for some other salamanders (e.g., *Desmognathus monticola, Plethodon wehrlei, D. o. ochrophaeus*). Although present-day populations of *Gyrinophilus* in southeastern Ohio show genetic influence from *p. duryi,* they appear to be different from either *p. duryi* or *p. porphyriticus* in some regards, indicating a certain amount of isolation at the present time. The Scioto River with its broad floodplain probably serves as an efficient barrier between *p. duryi* and *p. porphyriticus.*

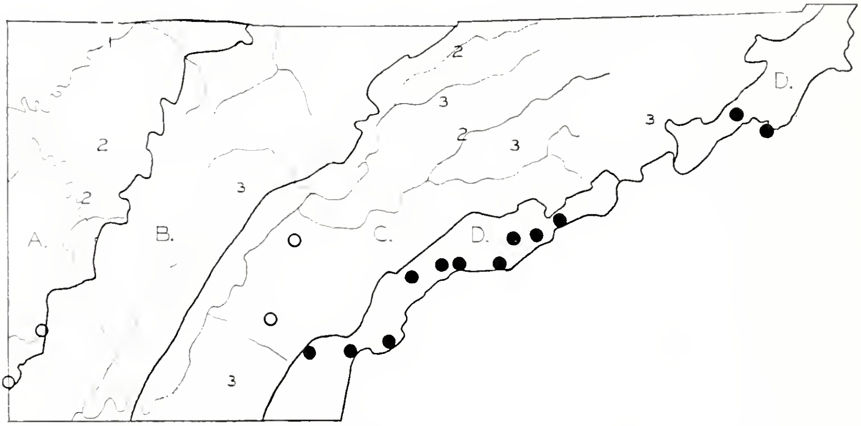

FIG. 22. Distribution of *Gyrinophilus* in Tennessee. Physiographic regions are the Eastern Highland Rim (A), Cumberland Plateau (B), Tennessee Valley (C), and Unaka Range (D). Numbers are those assigned to intergrades between *G. p. porphyriticus* and *G. p. duryi* as explained in the text; *p. danielsi* (solid circles); *palleucus* (hollow circles).

Cincinnati, Ohio, populations appear to be separated geographically from *p. duryi* and *p. porphyriticus* at present. The similarity between Cincinnati populations and those from the northeastern United States suggests that they are relics of those populations existing close to the glacial border, and that they were derived from those occurring in northeastern Ohio prior to glaciation. Although the Cincinnati populations show influence from *p. duryi,* the nearest records for the latter are Highland Co., Ohio, and Mason Co., Ky. It is possible that northeastern Ohio *p. porphyriticus* spread across north-central Ohio as advancing ice caused the Teays River to shift to the west (Coffey, 1961). With the union of the Teays and Hamilton rivers in eastern Ohio, *p. porphyriticus* could have spread up the Hamilton River drainage and occupied the present region of Cincinnati. With the reversal of the Hamilton (now Miami) and Teays (now Scioto, in part) rivers and their subsequent separation resulting from further glacial advances, the populations in Cincinnati were separated from those in northeastern Ohio.

It is not likely that populations connecting those in Cincinnati to *p. duryi* will be found. The only possibility is that additional populations may yet be found along the Ohio River Valley between Adams Co., Ohio, and Cincinnati. Specimens have been reported from the edge of the Outer Blue Grass region of Kentucky south of the Ohio River and east of Cincinnati (Maysville). Intergradation with *p. duryi* evidenced in Cincinnati populations may have occurred as *p. porphyriticus* spread across the north and west edges of *p. duryi* range just prior to the Nebraskan or Kansan glacial maxima.

As populations of northeastern United States *p. porphyriticus* were displaced southward through the Great Appalachian Valley by glacial advances, southward displacement probably also occurred along the outer Piedmont of Virginia, North Carolina, South Carolina, Georgia, and possibly Alabama. Thus, *p. porphyriticus* may have arrived in Alabama via two routes, although present material indicates that Piedmont populations of *p. porphyriticus* may not have spread westwardly entirely through Georgia. The specimens from farthest out on the Piedmont in North Carolina and Georgia show definite influence from *p. porphyriticus* (and the disputed Charleston, S.C., specimens are "pure" *p. porphyriticus*), but it is not yet clear whether this influence is a glacial relict, or whether populations of *p. porphyriticus* still extend along the outer Piedmont. I prefer the former interpretation, that *p. porphyriticus* extended down along the outer Piedmont during glacial advances and there intergraded with peripheral populations of *p. dunni.*

G. p. danielsi seems to have remained fairly distinct from *p. porphyriticus,* and no extensive intergradation seems to have taken place. Genetic contact with *p. porphyriticus,* except in the northern-most part of the range of *p. danielsi,* is indirectly through *p. dunni.* The only indication of intergradation between *p. porphyriticus* and *p. danielsi* is in populations just south of the Virginia–North Carolina–Tennessee border.

Intergradation between *p. danielsi* and *p. dunni,* its extent, criteria for recognition, and elevational influences, are poorly understood and may or may not have been influenced by glacial advances.

SUMMARY

The present review of the systematics of the North American plethodontid salamander genus *Gyrinophilus* is based on examinations of all available specimens (approximately 1450) and the literature dealing with the genus. Geographic variation in several characters (number of trunk vertebrae, ventral pigmentation, shapes and numbers of prevomerine and paravomerine teeth, numbers of premaxillary and maxillary teeth) is discussed.

Subspecies of two species are recognized, the epigean *G. porphyriticus* (4) and the cavernicolous *G. palleucus* (3). Nomenclature suggested for these salamanders is as follows:

Gyrinophilus porphyriticus porphyriticus

Gyrinophilus porphyriticus duryi
Gyrinophilus porphyriticus dunni
Gyrinophilus porphyriticus danielsi
Gyrinophilus palleucus palleucus
Gyrinophilus palleucus necturoides
Gyrinophilus palleucus gulolineatus

G. p. inagnoscus is placed in the synonymy of *p. porphyriticus, p. polystictus* in the synonymy of *p. danielsi,* and *G. lutescens* in the synonymy of *G. p. duryi.* Distribution of the recognized forms is summarized in Fig. 23.

The range of *palleucus* is broader than previously thought and is still very imperfectly known. *G. p. duryi* occurs in northeastern Kentucky and south-central Ohio, is a poorly delimited race, and intergrades over a wide area (southeastern Ohio, southern West Virginia, southwestern Virginia, eastern Tennessee, and probably extreme northwestern North Carolina) with *p. porphyriticus. G. p. porphyriticus* occurs throughout the northeastern United States and adjacent Canada, extends into northern Ohio, northeastern West Virginia, and central and eastern Virginia and has a range of influence extending down through the valley of the Tennessee River into Tennessee, northern Alabama, northwestern Georgia, and Mississippi, and south along the Piedmont into North Carolina, South Carolina, and Georgia.

G. p. danielsi occurs in the southern Appalachian Mountains, intergrading with *p. porphyriticus* and intergrades between *p. duryi* and *p. porphyriticus* in northwestern North Carolina and northeastern Tennessee, and with *p. dunni* at lower elevations in the southern edge of the Appalachian Mountains.

G. p. dunni occurs along the extreme southern margin of the southern Appalachian Mountains and adjacent Piedmont, and intergrades with *p. danielsi* along the mountain edge, and with *p. porphyriticus* to the west in northwestern Georgia and northern Alabama, and apparently to the south and east along the outer Piedmont.

Zoogeographical interpretation of present-day distributional patterns of *G. porphyriticus* is presented.

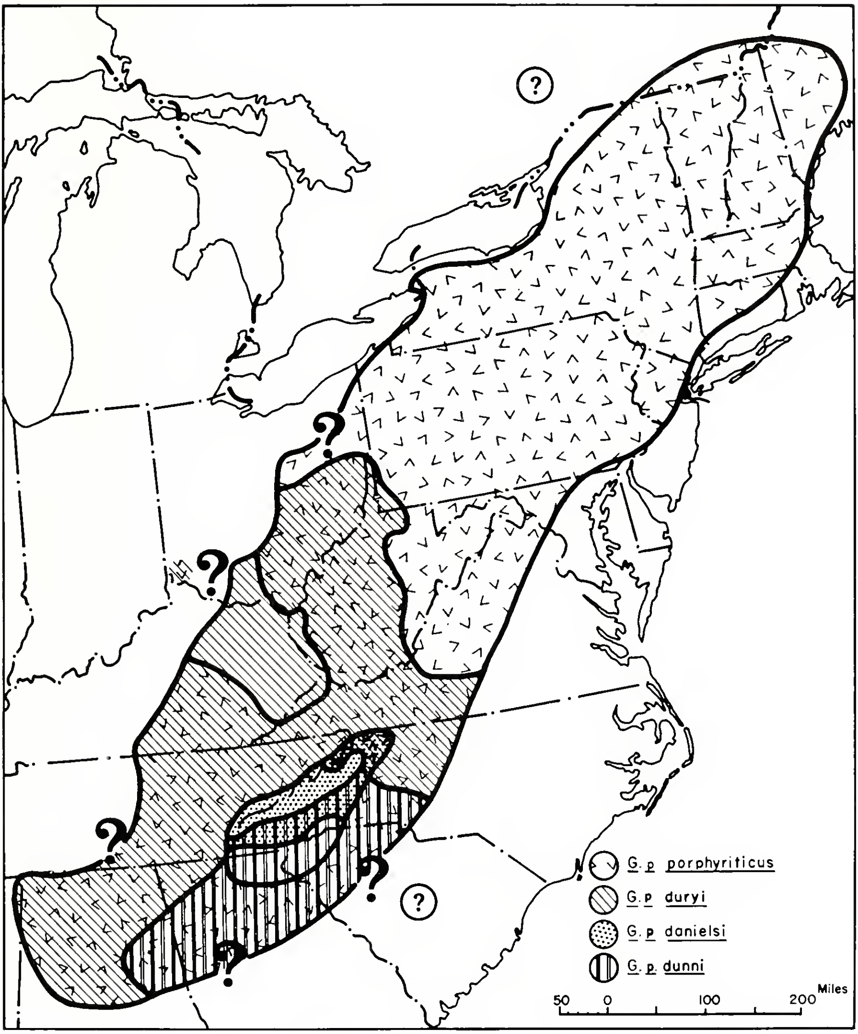

FIG. 23. Range of *Gyrinophilus porphyriticus*. Question marks indicate unknown distributional boundaries; encircled question marks indicate questionable localities.

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