MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 92

A Systematic Review of the Middle American Fishes of the Genus *Profundulus*

BY
ROBERT RUSH MILLER

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
September 28, 1955

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A SYSTEMATIC REVIEW OF THE MIDDLE AMERICAN FISHES OF THE GENUS *PROFUNDULUS**

INTRODUCTION

THE noteworthy richness and specialization of cyprinodont fishes in Middle America suggest that this group originated in the land mass connecting North and South America. These fishes, together with the characins and cichlids, comprise the bulk of the fresh-water fish fauna of that region. One small group of killifishes, allied to the more widespread genus *Fundulus*, is the subject of this contribution.

Species of the genus *Profundulus* typically inhabit the mountain streams of Middle America, where they are most abundant at altitudes between 3,000 and 7,000 feet. At the higher elevations they constitute the only native fishes and are here less restricted in habitat than in the lowlands. The fish are small, generally between three and four inches in total length, but exceptional individuals may reach five inches (127 mm.). The genus is distributed along both slopes of Middle America, from near Acapulco, México, to western Honduras on the Pacific side and from the Isthmus of Tehuantepec to the Río Motagua, Guatemala, on the Atlantic slope (Map 1).

The separation of *Profundulus* and *Fundulus* as distinct genera is fully confirmed by a study of the abundant material of each genus that has been made available to me. A critical comparison of the two genera is presented in Table I, p. 15.

Profundulus is readily separable into two distinct species groups, the origins of which are associated with the complex geological history and ecological diversity of southern México and northern Central America. Each group has undergone differentiation, some of which has taken place at the species level; for the most part, however, the material presents a bewildering array of local populations reminiscent of the type of variation characteristic of such a plastic group as the salmonoid fishes. With a few specimens from scattered localities at hand, the systematist may feel certain that he is dealing with distinct species. After studying more than 9,000 specimens, however, I am convinced that only four unquestionably distinct species may be recognized, and that one additional species may be admitted. Three of the species (*punctatus*, *guatemalensis*, and *labialis*) show considerable intraspecific variation. This seems to be mostly at random and thus defies orderly arrangement, even though some of the differences noted probably have a genetic basis, at least in part. Such populations may represent distinct races, or incipient subspecies or species, or they may result directly from environmental responses. Their status could be clarified further by experimental studies, although experimental taxonomy does not provide the whole answer to systematic problems.

In preparation for this revision it was my good fortune to spend five

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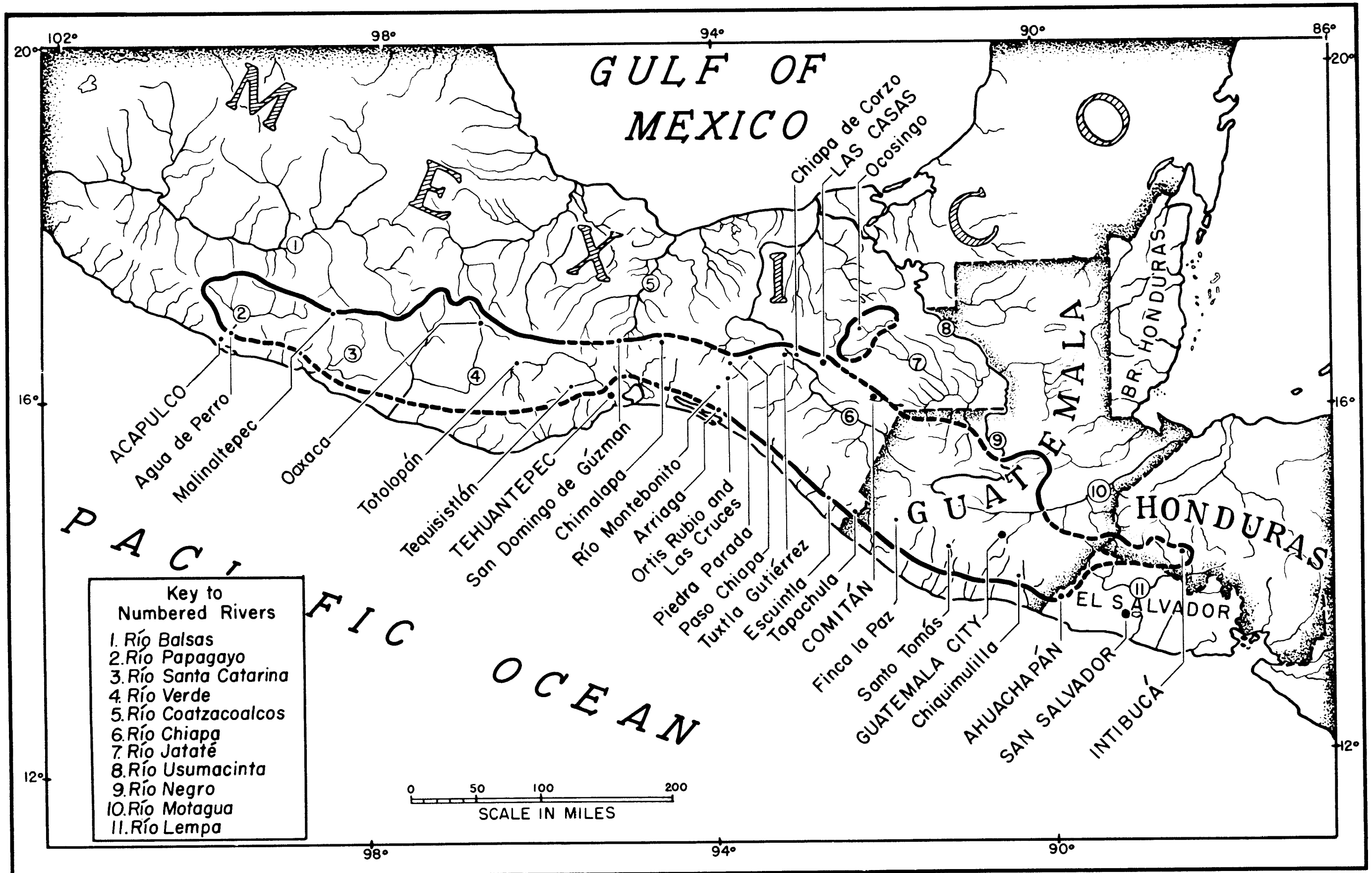


Map 1. A section of Middle America, showing the approximate distribution of the genus *Profundulus*. In those places from which no specimens are available the limits of the range are represented by a broken line.

months in Guatemala while on the staff of the Smithsonian Institution. This field work, sponsored through the co-operation of the U. S. Fish and Wildlife Service and the Guatemalan government, enabled me to obtain more than 7,000 specimens of *Profundulus* at 72 stations. First-hand knowledge of the life appearance, habitat, and ecology of the Guatemalan species has proved invaluable in the present study. A discussion of the ecology of the genus is intended for separate publication.

Dr. Leonard P. Schultz and his staff have generously loaned all of the material of *Profundulus* in the U. S. National Museum (USNM) and have also presented series of the Guatemalan material to the University of Michigan by exchange; through the courtesy of the authorities of the Chicago Natural History Museum (CNHM) and Loren P. Woods important material has been examined; Dr. Ethelwynn Trewavas made it possible for me to study the pertinent material in the British Museum of Natural History (BM); Dr. Deckert of the Berlin Museum and Dr. Erna Mohr of the Hamburg Museum co-operated in sending the University of Michigan Museum of Zoology (UMMZ) two paratypes of *P. balsanus;* and Dr. José Alvarez has very kindly presented two paratypes of *Tlaloc mexicanus*. Mrs. Phyrne Squier Russell, of the Academy of Natural Sciences of Philadelphia (ANSP), made it possible for me to study type specimens in that institution. Material at the Stanford Natural History Museum (SNHM) was examined there by courtesy of Dr. George S. Myers and Dr. Margaret Storey. Ancil D. Holloway, aquatic biologist of the U. S. Fish and Wildlife Service, and Señor Julio Midence, Guatemalan assistant and interpreter, were of constant help in the field work. I also wish to thank Dr. Stillman Wright, acting chief, Office of Foreign Activities, U. S. Fish and Wildlife Service, for permission to reproduce Map 2. Dr. John Van Oosten kindly translated the paper by Hoedeman and Bronner (1951). I wish particularly to thank L. C. Stuart, N. E. Hartweg, Myron Gordon, James W. Atz and associates, Salvador Coronado, and Kenneth L. Pike, who collected *Profundulus* over a series of years extending from 1932 to 1949. Dr. Stuart, in particular, fulfilled specific requests for me and made available critical aerial maps, and I have benefited from his broad knowledge of Guatemala. Dr. Archie Carr obtained the single collection of *Profundulus* from Honduras. Peggy Hinson drafted the graphs (Figs. 3-6) and William E. Duellman kindly inked them. My wife, Frances H. Miller, has been indispensable in the statistical computations, the work with X-rays, and in proofreading.

MATERIALS AND METHODS

This revision of *Profundulus* is based upon an examination of 9,340 specimens from throughout the known range of the genus (Map 1). About 7,500 are from Guatemala, and the remainder come mostly from southern México, with a single collection each from El Salvador and Honduras. *P. punctatus* is represented by 897 specimens; *P. guatemalensis* by 4,432; *P. labialis* by 3,220; *P. candalarius* by 275; and *P. hildebrandi* by 516 specimens (see Material Examined, p. 56).

The type material of *P. labialis, P. guatemalensis,* and *P. pachycephalus* in the British Museum was studied and lectotypes of the first two species have been selected. The holotype and allotype of *P. candalarius,* the holotype and paratypes of *P. oaxacae,* the holotype and paratypes of *P. scapularis,* two paratypes of *P. balsanus* and two of *Tlaloc mexicanus* have been examined. I also collected large series of topotypes or subtopotypes of *P. labialis, P. guatemalensis, P. punctatus,* and *P. scapularis.* Topotypes of *P. pachycephalus* also have been studied, and the type material of *P. hildebrandi* has been re-examined. Additional material of *P. candalarius* from México, kindly collected by Salvador Coronado, has made possible the clarification of its status.

Two new characters of taxonomic significance have been utilized. Each premaxilla in *Fundulus* and *Profundulus* has a backward-extending median process, the shape of which is quite different in these two genera (Fig. 1, p. 10). The median hypural plate, with which the urostyle is fused, appears as a single bone in *Fundulus,* but is partly divided by an open groove in *Profundulus* (Pl. II, A-C). These two structural differences may make it possible to place with confidence fossil species referred to *Fundulus.*

In the synonymies, only those references which contain original data are listed. It seems unnecessary to refer to works in which the observations of other authors have been merely repeated. Thus, for example, I do not list under the synonymy of *Profundulus punctatus* the account given by Jordan and Evermann (1896: 637), since this is taken directly from Günther.

The methods of counting and measuring are the same as those used in my study of *Cyprinodon* and *Empetrichthys* (Miller, 1948: 9-13) and are not repeated in detail here. The last ray of the dorsal and anal fins was always regarded as a double ray, divided to the fin base, and was counted as a single ray (rather than two rays, as was Günther's practice). A notation was made of the number of branched and unbranched rays in these fins. Only the principal caudal rays, the branched rays plus one unbranched ray on either side, were tabulated. The scales in the lateral series were counted from the first scale in contact with the shoulder girdle to the scale at the structural base of the caudal fin. If the crease formed by moving the caudal fin from side to side lay near the middle of the last scale or posteriorly, the scale was included in the count. Scale counts, other than those along the side, were often so unreliable because of numerous regenerated scales that many of these data are not presented. The scale count between the lateral series and the middle of the back included the scale on the mid-line of the back but not the one in the lateral series (Table II). The scale count around the body was made, in zigzag fashion, about two scales in advance of the pelvic fins; that around the caudal peduncle was similarly made around the slenderest part. These two counts yielded bimodal frequency distributions (Table XIV) such as characterize certain populations of *Cyprinodon* (Miller, 1948: 79). The total number of gillrakers on the first branchial arch (right side only), including all rudiments, was recorded without a separate tabulation for the two limbs. The urostyle was included in the vertebral counts, which were obtained largely by means of X-ray photographs.

A close, positive correlation between the number of vertebrae and the number of lateral scales was found in *Profundulus* (Tables XIII, XIV). The agreement is usually perfect, as it is for the lectotypes of *P. guatemalensis* and

P. labialis (Pl. II). When a precise scale count was not possible, the vertebral number could be taken as an accurate indication of the number of lateral scales. Garman (1895: 159) pointed out this correlation for many species of Cyprinodontes.

GENUS *PROFUNDULUS* HUBBS

Profundulus Hubbs, 1924: 12. Type by original designation, *Fundulus punctatus* Günther.
Tlaloc Alvarez and Carranza, 1951. Type by original designation, *Tlaloc mexicanus* Alvarez and Carranza (= *P. labialis*).

Prior to 1924 the members of this genus of cyprinodontid fishes were variously assigned to the genera *Fundulus, Adinia,* and *Zoogoneticus,* the last a member of the exclusively Mexican family Goodeidae (Hubbs, 1924: 13; Hubbs and Turner, 1939). The confusion concerning the relationships of *Profundulus* was largely due to lack of material, for between 1866 and the early part of 1900 the species were known almost solely from the type material in the British Museum (Natural History). Uncritical shifting of the species to unrelated genera also contributed to an erroneous picture of relationships, and misidentifications caused further confusion. Thus Garman (1895: 100-101), in his monographic review of the cyprinodonts, synonymized all the known species of *Profundulus* with *Fundulus parvipinnis* Girard, an action which surely stemmed in large part from lack of material. Even though a wealth of specimens has been available to me, certain questions still remain unanswered — for example, the precise status of *P. punctatus, P. guatemalensis,* and *P. balsanus* Ahl. Except for my preliminary account (Miller, 1950: 27-28), no author had previously recognized two species groups in the genus.

The genus *Tlaloc,* described by Alvarez and Carranza, is synonymous with *Profundulus,* for it agrees in all important characters with that genus. *Tlaloc* was misplaced by its describers in the tribe Rivulini (Cyprinodontidae) from which it is immediately excluded by having too broad a preorbital, no vomerine teeth, and no pseudobranchiae (Myers, 1931: 250). Examination of two paratypes of *Tlaloc mexicanus* (UMMZ 162154) from the type locality, and of a specimen of *P. labialis* (UMMZ 161767) from El Real, Chiapas, where a single paratype of *Tlaloc* was also collected (Alvarez and Carranza, 1951, Fig. 1), reveals that this nominal genus and species is identical with *Profundulus labialis* (see discussion under that species on pp. 43-44.

Profundulus is a member of the family Cyprinodontidae and of the tribe Fundulini, as discussed by Myers (1931: 9-10). His diagnosis of the subfamily Fundulinae must be modified in two particulars: (1) there are more than 34 vertebrae, for *Profundulus* has as many as 39 (Table XIV), at least eight species of *Fundulus* have as many as 37, and two species of that genus, *F. stellifer* (Jordan) and *F. seminolis* Girard, have up to 38 (Garman,[1] 1895:

[1]It seems safe to assume that Garman did not include the urostyle in his vertebral counts; I have therefore added one to his counts to bring them in line with my own.

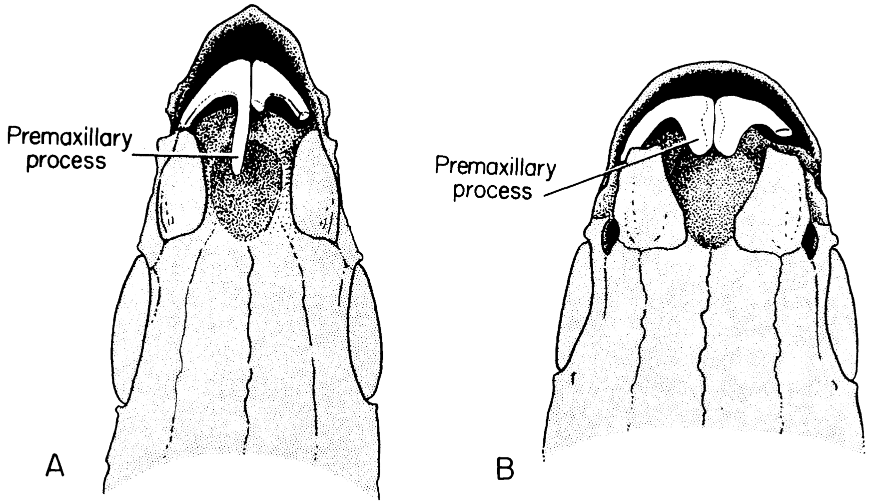


Fig. 1. Dorsal view of anterior part of skull of *Fundulus* (A) and *Profundulus* (B) to show the ascending premaxillary process. Based on semidiagrammatic sketches of *Fundulus similis* and *Profundulus hildebrandi*. For variation in this structure, see text.

103, 108; Clothier, 1950: 41; many original counts); and (2) the caudal fin is scaled more than halfway to the tip in some species of *Profundulus*, e.g., *P. guatemalensis*. This is also true of at least one species of *Austrofundulus*, as pointed out by Myers (1932: 160) and later (Myers, 1942: Fig. 13) figured by Ortiz. Also, as Myers has noted, the teeth of the Fundulinae, though typically conical, may be bicuspid (as in *Crenichthys*); if the Cyprinodontinae is combined with this subfamily, as may be desirable, then the teeth should be described as conical, bicuspid, or tricuspid. *Carrionellus*, from the Tertiary of Ecuador (White, 1927), has tricuspid teeth but otherwise looks like a funduline and may prove, on further study, to bridge the small gap that is currently used to separate the Cyprinodontinae from the Fundulinae.

While this paper was being written, Hoedeman and Bronner (1951) erected the tribe Profundulidi to include *Profundulus* and *Adinia* and the Old World genera *Valencia* and *Kosswigichthys*. I regard this as an unnatural assemblage which was united, in part at least, through misinterpretation of characters and a failure to appreciate the close affinities between *Fundulus* and *Profundulus*. For example, of the included genera only *Kosswigichthys* was stated to have a genital pouch in the female, but *Adinia* also has such a pouch surrounding the first three to four anal rays. Thus two of the genera have this structure while the other two lack it, despite the fact that the authors claimed that the absence of a genital pouch is among the most important characters of their tribe. Moreover, Myers (1931: 249) wrote of *Valencia*, which has a narrow preorbital: " . . . this genus may represent the ancestral stock from which the Rivulini have sprung." The preorbital is also narrow in *Kosswigichthys*, although not so shown in the illustration (Fig. 22) given by Hoedeman and Bronner. Steinitz (1951: 121) regarded *Valencia* as a generalized, relatively old type, in contrast to the much more recently evolved and highly specialized *Kosswigichthys*. An examination of specimens of *Valencia hispanica* (kindly loaned by the Harvard Museum of Comparative Zoology) and of syntypes of *V. letourneuxi* (received through the kindness of Dr. León Bertin) convinces me that this genus is a generalized, independent derivative probably not closely related to any New World genus. For these reasons I suggest that the tribe Profundulidi, as defined by Hoedeman and Bronner, be abandoned.

Diagnosis. — Teeth conical, curved inward, in several irregular rows on each jaw, the outer row enlarged. Body rather robust, elongate, with the general aspect of *Fundulus* or *Umbra*, the interorbital broad and usually convex (typically concave or nearly flat in *P. punctatus*). Dorsal and anal fins posterior, usually rather long and low, the origin of the dorsal over or almost over that of the anal. Anal fin lower in the adult male than in either the adult female or the young. Oviduct of mature female forming a very weak genital pouch, the lateral rims of which are scarcely produced so that they surround not more than the first anal ray. Preorbital broad and naked or narrow and scaled. Preopercular-mandibular sensory canal system (Fig. 2) connected or nearly so, but frequently slightly separated (most consistently so in *P. candalarius*). Each anterior nostril set at the end of a tubelike pouch. Ascending premaxillary process (Fig. 1) short and broad and bluntly rounded at the tip. Dorsal rays 10 to 16, of which the first 1 to 3 (usually 2) are unbranched;[2] anal rays 11 to 18, of which the first 1 to 3 (usually 2) are unbranched; pectoral rays 15 to 22; pelvic rays 6 (rarely 5 or 7); and principal caudal rays 17 to 25 (15 to 23 branched). Scales in lateral series 31 to 39; scales around body 24 to 36; scales around caudal peduncle 16 to 25. Vertebrae 31 to 39 (including urostyle), the first rib attached to the second vertebra. Median hypural plate divided into subequal parts by an open groove (Pl. II, A-C).

Range. — On the Pacific slope, from the Río Papagayo of Guerrero, southeastern México, southward to western Honduras (Río Lempa drainage), on the coastal plain as well as in the mountains; on the Atlantic slope, from the Isthmus of Tehuantepec to the Río Motagua, Guatemala, only in the highlands (Map 1). Altitudinal range from about 300 feet (Pacific versant) to 8,000 feet.

Numerous collections made recently (1949) in the Atlantic highlands of Honduras, by Dr. Archie Carr, failed to reveal *Profundulus* in that area. The presumed occurrence of *P. balsanus* Ahl (1935) in the Río Balsas, Guerrero, México, has not been confirmed (Miller, 1950: 29), and the record of *"Fundulus guatemalensis"* from western Ecuador (Günther, 1866: 321; Eigenmann and Eigenmann, 1891: 64) clearly represents an erroneous locality label (see Hildebrand, 1925: 254; and p. 31). The "*Fundulus* spec. ? aus Venezuela," reported by Ladewig (1932), turned out to be *Profundulus punctatus* from Finca del Rosario, southwest of Yepocapa (Map 2), on the Pacific slope of Guatemala (Myers, 1935: footnote 1; same specimens, USNM 94217, examined by me).

Comparison with *Fundulus*. — *Profundulus* was considered by Hubbs (1924:

[2]A single exception was noted. In a paratype of *P. guatemalensis* (BM 1864.1.26 189B), from Lake Dueñas, Guatemala, all the dorsal rays are branched.

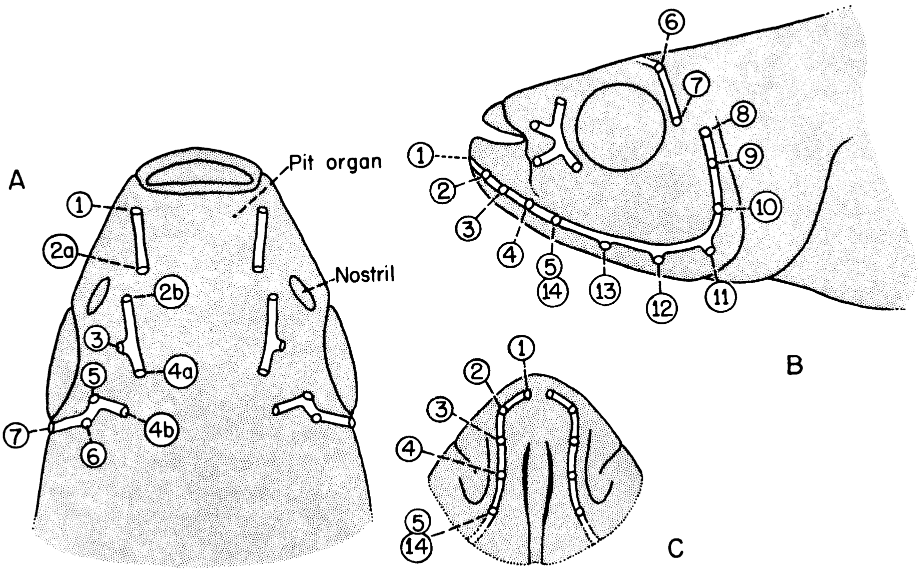
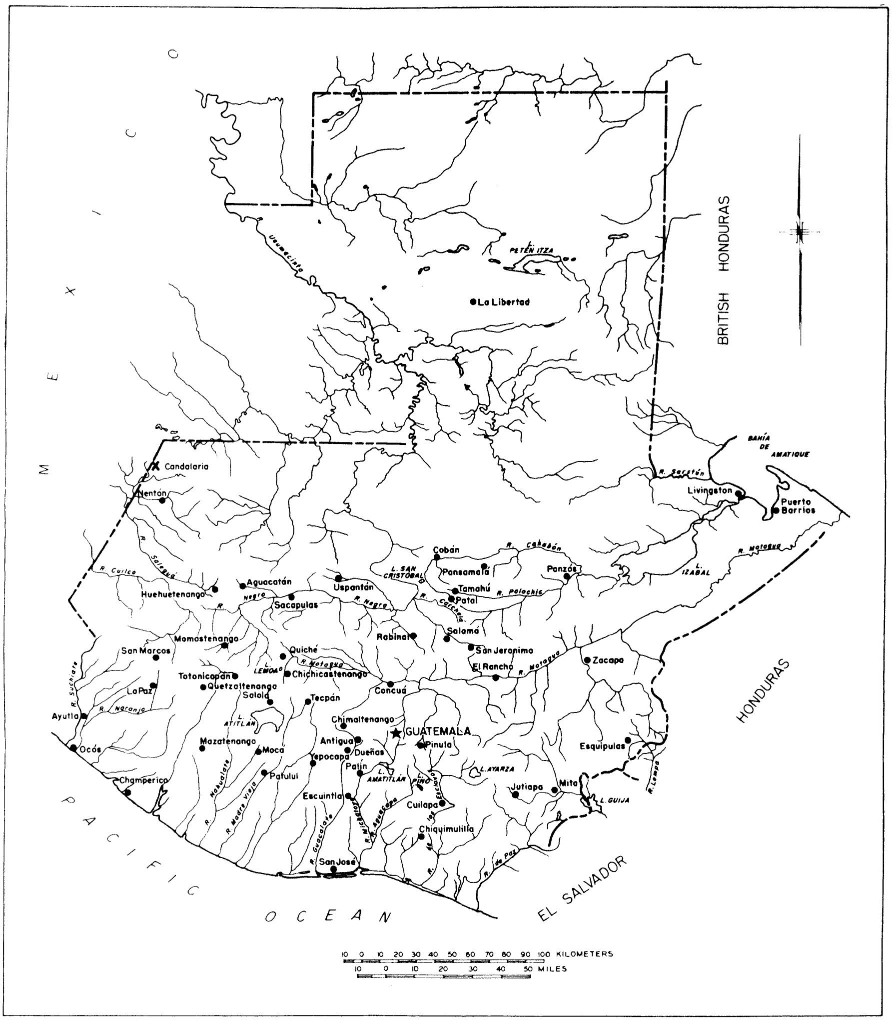


Fig. 2. Lateral-line system of sensory canals and pores on the head of *Profundulus* (compare with Gosline, 1949, Pl. II). Based on semidiagrammatic sketches of *P. punctatus*. A, the supraorbital canal, 1-4a, is broken between 2a and 2b and is separated from the postorbital canal between 4a and 4b. B, the mandibular canal, 1-5, is joined to the preopercular canal, 8-14, which is separated from the postorbital canal, incompletely represented by 6 and 7. The preorbital canal always has 4 pores. C, view of the chin to show the 5 mandibular pores and the lowermost preopercular pore. See Table I and text for variation in these structures.

12) to be closer to an ancestral cyprinodont type than any other American genus of this group. There is no question that it is most intimately related to *Fundulus* (Table I). In drawing the following comparison I studied specimens of the 27 species of *Fundulus* that I tentatively recognize (Miller, 1955), including the two species of *Plancterus* – herein regarded as a subgenus of *Fundulus*.[3] I have not examined specimens of *F. fonticola* Valenciennes but have studied the holotype and paratype of *F. antillarum* Fowler; the status of these nominal forms is very doubtful (see letter by Myers in Rivas, 1948: 216-17).

Two of the more important characters distinguishing the genera were pointed out by Hubbs (1924: 12); subsequently the diagnostic difference in the sensory canal systems was described by Gosline (1949: 4, 5, 11, 14) and has been studied further by me. Three characters – the shape of the

[3]In surveying the species of *Fundulus*, I am unable to justify generic recognition of *Plancterus* on the proposed basis of the longer, extensively convoluted digestive tract, weaker and slenderer pharyngeal teeth, or the more restricted attachment of the gill-membranes (Hubbs, 1926: 14). The fundamental points of agreement between the two genera are more impressive than are the few differences noted; some of these, moreover, are shared by other species currently placed in *Fundulus*, and others are clearly nutritional modifications.



Map 2. Drainage map of Guatemala showing localities mentioned in the text. Reproduced, with modifications, by courtesy of the United States Department of the Interior (see U. S. Fish and Wildlife Service, Special Scientific Report: Wildlife No. 5, 1950: 140).

premaxillary process, the nature of the hypural plate, and the number of gillrakers — are used here for the first time as additional aids in distinguishing the two genera (Table I). The ranges of these genera are mutually exclusive, for *Fundulus* reaches the mainland of Middle America only along the tip of the Yucatán Peninsula and on the eastern coastal plain of México, where no *Profundulus* has been reported.

Certain other characters, such as the position and length of the fins, were regarded by Hubbs as distinctive of *Profundulus*. However, these features are too variable for use in separating *Profundulus* from *Fundulus*. Thus the anal fin has 11 to 18 rays in *Profundulus* and 8 to 16 rays in

Fundulus (including *Plancterus*). The dorsal and anal fins are far back on the body in *Profundulus*, but certain species of *Fundulus*, notably *F. albolineatus*, *F. chrysotus*, *F. notti* , *F. jenkinsi*, *F. luciae*, *F. notatus*, *F. olivaceus*, *F. rathbuni*, *F. sciadicus*, and *F. similis*, also have these fins placed posteriorly. The interorbital is generally more convex in *Profundulus* than it is in *Fundulus*, but the difference is a subtle one and does not hold, for example, when *P. candalarius* and *P. punctatus* are compared with *F. similis* and *F. parvipinnis*.

The sensory canals and pores on the head of *Profundulus* (Fig. 2) are rather uniform in pattern and development among the species. The connection between the preopercular and the mandibular series is not infrequently broken, but the separation is generally slight except in *P. candalarius*, in which these two canals are typically separated. The preopercular-mandibular canals are almost invariably joined in *P. hildebrandi* and are typically connected in *P. punctatus* and *P. guatemalensis*, but the connection is more variably developed in *P. labialis*. As Gosline (1949: 5, 14) pointed out, the canal and pore systems of *Fundulus* and *Profundulus* are otherwise very similar, and three species of *Fundulus* (*confluentus*, *majalis*, and *similis*) closely resemble *Profundulus* in the pore and canal arrangement.

The genital pouch or sheath is developed only in mature females. Several species of *Fundulus* have a moderate to well-developed sheath (as in *F. heteroclitus*), but the structure typically does not extend far out onto the anal fin. Some species, such as *F. confluentus* and *F. notti* , have a very short pouch (Hubbs, 1931: 5) which may even appear to be almost absent, but closer inspection will show that it surrounds at least the first two, and usually several, rays of the anal fin. The structure is uniformly weak or obsolete in *Profundulus*.

The anal fin of the mature male of *Profundulus* is not elevated as it is in the female, especially females of the *P. labialis* species group. In *Fundulus*, almost without exception, this fin is much higher in the mature male than it is in either the female or young. *F. zebrinus*, *F. kansae*, and *F. confluentus* approach *Profundulus* in this character.

As in other cyprinodont fishes (Starks, 1904: 258), the premaxilla in *Fundulus* and *Profundulus* has a backward-extending process on the median line of the snout, the ascending premaxillary process. In *Profundulus*, this is short and broad and usually truncate to broadly rounded and little narrowed at the tip; whereas in *Fundulus* it is typically long, narrow, and pointed at the tip (Fig. 1; see also Gregory, 1933: 218, Fig. 97B). The shape of this structure is variable among the following species of *Fundulus*: *F. notti* — fairly broad, but also long and pointed; *F. grandissimus* — relatively broad, but long and pointed at the tip; *F. seminolis* — short, but narrow; and *F. notatus* and *F. olivaceus* —comparatively short, broad, and little pointed, but less so than in *Profundulus*.

The terminal part of the vertebral column in *Fundulus* and *Profundulus* consists of the urostyle, median hypural plate, and associated elements (Hollister, 1940: Fig. 5). The urostyle and median hypural appear to be completely consolidated. In *Fundulus*, the median hypural is fused into a single, fan-shaped bone with, at most, a weakly developed suture medially. In *Profundulus* the fusion is incomplete (Pl. II, A-C), so that an open groove

TABLE I

COMPARISON BETWEEN *PROFUNDULUS* AND *FUNDULUS*

See discussion of these characters in text.

Character	*Profundulus*	*Fundulus*
Preopercular-mandibular sensory canals (Fig. 2) . .	Typically connected or nearly so; normally slightly separated in one isolated species	Never connected; moderately to widely separated
Genital pouch of mature female	Weak to obsolete; lateral rims of genital aperture scarcely produced, surrounding not more than first anal ray	Weakly to well developed; lateral rims at minimum forming a pouch surrounding the first 2 anal rays
Gillrakers (Table XIV) . . .	More numerous, 14 (rarely) to 23, typically 16 or more	Fewer, 4 to 14 (rarely), typically fewer than 12
Ascending premaxillary process (Fig. 1).	Short and broad and only slightly narrowed at tip	Typically long and narrow, rarely short and narrow*
Median hypural (see Hollister, 1940: 100, and Pl. II, A-C)	Incompletely fused into subequal parts by an open groove extending backward from tip of urostyle about 1/2 to 2/3 distance to tip of hypural	Fused (except possibly in early life); at most a weak suture on one side
Anal fin of adult male	Lower than that of young or adult female	Higher than that of young or adult female

*In the few species in which it is relatively broad, this process is still more elongate in *Fundulus* than it is in *Profundulus* (see text).

separates the median hypural fan into two subequal parts and spreads backward from the tip of the urostyle for a variable distance. Usually, it extends for about one-half the distance from the tip of the urostyle to the posterior margin of the hypural fan, although in some specimens it was seen (on X-ray photographs) only as a slit at the tip of the urostyle and in others it was developed over about two-thirds the distance to the margin of the hypural fan. At its weakest development, the median slit closely resembles that figured for *Gambusia affinis holbrooki* or *Lebistes reticulatus* (Hollister, 1940: Figs. 12, 15). The study of the hypural plate was made largely through the use of X-ray photographs, with confirmation of the condition noted by careful dissection of a single specimen each of *Fundulus* (*similis*) and *Profundulus* (*labialis*). The examination was rather thorough for *Profundulus* (many radiographs of all species) but included only the following species of *Fundulus: albolineatus, diaphanus, grandissimus, heteroclitus, kansae, parvipinnis, persimilis, seminolis, similis, stellifer,* and *zebrinus.*

A thorough revision of *Fundulus,* a comparative osteological study of the two genera, and a better knowledge of the fossil record are needed in order to determine which species of *Fundulus* may be the nearest relative of *Profundulus.* We cannot be certain, for example, that *Fundulus detillai*[4] and *F. sternbergi,* as described by Hibbard and Dunkle (1942) and Robertson (1943), respectively, from the Middle Pliocene of Kansas, may not belong to *Profundulus.*

KEY TO THE SPECIES OF *PROFUNDULUS*

1a. — Preorbital nearly covered with well-developed scales; humeral spot present; basal one-half or more of caudal fin densely scaled; anal fin of mature female only moderately elongated (*P. punctatus* species group; subgenus *Profundulus*) 2

- 2a. — Body of adult with conspicuous rich brown spots[5] (Pl. I, B-C, F) on scales, aligned to form longitudinal rows along sides from near pelvics usually to well out onto caudal fin; head conical, its dorsal surface concave to nearly flat . . *punctatus* (p. 17)
- 2b. — Body at all ages without brown spots (Pls. III-IV) along the scale rows; head typically rectangular and more arched, its dorsal surface generally much rounded . . *guatemalensis* (p. 25)

1b. — Preorbital usually naked, frequently with one or two isolated, embedded scales; humeral spot absent; less than basal half of caudal fin densely scaled; anal fin of mature female usually markedly elongated (*P. labialis* species group; subgenus *Tlaloc*) 3

- 3a. — Lower jaw broad, heavy and protruding so that upper jaw is included; body uniformly slender, with a dark spot at base of caudal fin (Pls. V-VI). . . . . *hildebrandi* (p. 46)
- 3b. — Lower jaw not broad and heavy but like upper jaw, and either equal in forward projection or included; body deeper, no dark spot at base of caudal fin 4
  - 4a. — Lateral scales typically 36 to 38 (34-39), vertebrae usually 36 or 37 (35-39); predominantly six scales from mid-line of back to (but not including) scale in lateral series (Pls. VII-VIII). . . . . *labialis* (p. 31)
  - 4b. — Lateral scales typically 34 (33-36), vertebrae usually 34 (33-35); five scales from mid-line of back to (but not including) scale in lateral series (Pl. IX) . . . . *candalarius* (p. 44)

[4]Incorrectly proposed as *F. detillae.*

[5]Usually absent in young, occasionally weak or undeveloped in half-grown, and rarely obsolete in small adults (Pl. I, A).

THE *PUNCTATUS* GROUP (SUBGENUS *PROFUNDULUS*)

The distinctive characters of the members of this species group are brought out in the preceding key and in Table II. The two species recognized, *P. punctatus* and *P. guatemalensis,* are closely related, allopatric forms. Some might feel that these species should be united, as was done by Regan (1906-8: 78) and, provisionally, by Hubbs (1924: 13); however, I have been able to identify with certainty at least 95 per cent of all populations of the two types, and each evidently constitutes a natural geographic unit. Each species exhibits incipient subspeciation, some of which might be recognized nomenclatorially.

P. guatemalensis is nearly restricted to the Guatemalan Highlands, or Altos (Map 2), where it is usually found at elevations between about 2,800 and 5,000 feet. In the Río Motagua basin (Atlantic slope) it was taken west of El Rancho as low as approximately 2,000 feet and was found down to 1,750 feet in the Río Michatoya north of Escuintla, on the Pacific versant. No individuals were taken above 6,500 feet. *P. punctatus,* on the other hand, is confined (in Guatemala) to the Pacific Coastal Plain and the outer slopes of the Cordillera, generally to the westward of the range of *guatemalensis* and typically well below 4,000 feet. Furthermore, I have especially sought for and failed to find intergradation. The highland form, *guatemalensis,* appears to penetrate the region occupied by *punctatus* in only two places (Map 2): the Río Michatoya near Escuintla (USNM 144400 and UMMZ 166696) and, evidently, the basin of the Río de los Esclavos at Finca La Gloria, 13 km. ENE of Chiquimulilla (UMMZ 158449-450). At neither of these localities do the species occur together. The series from near Escuintla closely resembles highland samples of the species; the material from Finca La Gloria comprises three poorly preserved adults and eight young to small adults and is insufficient to render a positive determination, but the specimens apparently are *guatemalensis.*

The assumption (Hubbs, 1924: 13) that *guatemalensis* was based upon "well-nourished, pale-colored lake specimens of *punctatus*" is conclusively disproven by both field and laboratory studies, for *Profundulus* is a stream fish that shuns lakes and, with few exceptions, the two types are consistently and strikingly different in body spotting (Pls. I-IV). Authors have apparently failed to realize that the name *punctatus* refers to the distinctive dark spots on the body under the scales, rather than to the inconsistently developed and much less conspicuous spotting on the fins.

Profundulus punctatus (Günther)

Pls. I – II

Fundulus punctatus. — Günther, 1866: 320-21 (orig. descr. based on one spec.; type loc. Chiapám [coastal lagoon near Champerico], Guatemala); 1868: 482, Pl. 84, Fig. 5 (redescr. with fig.). Regan, 1906-8: 78 (in part; redescr. based partly on type; Gúzman, Tototolopán, Tequisistlán, México — see Map 1 herein). Meek, 1907: 136 (Mazatenango and San José de Idolo, Guatemala). Fowler, 1916: 417 (central Guatemala; Cope. Material not seen by me).

Profundulus punctatus. — Hubbs, 1924: 13-14 (in part; synonymy; descr. of Guatemalan material). Miller, 1950: 28 (diagnostic characters).

Fundulus pachycephalus. — Günther, 1866: 321-22 (orig. descr.; type loc. L. Atitlán, Guatemala); 1868: 483, Pl. 84, Fig. 6 (redescr. with fig.). Meek, 1904: 104 (L. Atitlán sample synonymized with *punctatus*); 1907: 136 (synonym of *punctatus*). Regan, 1906-8: 77 (redescr. of types). Hubbs, 1924: 13 (synonym of *punctatus*). Miller, 1950: 27 (suspected to be identical with *punctatus, sensu stricto*).
Zoogoneticus pachycephalus. — Meek, 1902: 94 (name only).
Fundulus parvipinnis (misidentification). — Garman, 1895: 100 (in part; *punctatus* in synonymy).
Fundulus oaxacae. — Meek, 1902: 90, Pl. 20 (orig. descr.); 1904: 104-5, Fig. 28 (redescr.). Regan, 1906-8: 78 (synonym of *punctatus*).
Profundulus oaxacae. — Hubbs, 1924: 15 (provisionally recognized). Miller, 1950: 27-28 (recognized).
Fundulus spec. ? aus Venezuela. — Ladewig, 1932: 497-98, 1 fig. ("ein Bach in Venezuela in 1000 m. Höhe"). Myers, 1932: 161 (thought to be an *Austrofundulus*); 1935: 7, footnote 1 (corrected locality: Finca del Rosario, 1000 m., SW of Yepocapa, Pacific slope of Guatemala; identified as *P. punctatus*).
?*Profundulus balsanus*. — Ahl, 1935: 108 (orig. descr.; type loc. Malinaltepec, Guerrero, México). Miller, 1950: 28-29 (validity uncertain; doubtful if from Río Balsas drainage).
Profundulus scapularis. — Fowler, 1936: 522, 524, Figs. 21-23 (orig. descr.; type loc. Finca Mocá, on S slope Volcán de Atitlán, Guatemala; in part, types only). Miller, 1950: 27 (topotypes examined; synonym of *punctatus*).

Synonyms. — The nominal species *P. pachycephalus*, known only from Lake Atitlán and now apparently extinct there, is, as I recently suggested (Miller, 1950: 27), a synonym of *P. punctatus* rather than of *P. guatemalensis*. Regan (1906-8: 77) recognized *pachycephalus* as valid on the basis of the broad interorbital and large eye ("snout not longer than eye"). Günther (1866: 321) erred in stating that *pachycephalus* has a smaller eye than *guatemalensis* and that the snout is longer than the eye, as is clearly shown by the subsequent figure (Günther, 1868: Pl. 84, Fig. 6) and by study of the types. Günther correctly stressed the thick head, with broad interorbital, but material collected in 1902 by Gustav Eisen (USNM 127088) fails to confirm this distinction. An examination of the three type specimens[6] (BM 1864.1.26.187A-C), males 47.6, 55.0, and 60.4 mm. standard length, plus a fourth nontype male (BM 1864.1.26.187D), 53.5 mm. long, convinces me that their unusually broad, heavy heads and large eyes are an environmental response, perhaps due to emaciation in the relatively cool and unproductive waters of Lake Atitlán; or, perhaps more plausibly, the larger parts may have resulted from rapid development in or near the hot springs that occur or formerly occurred in certain areas of the lake (McBryde, 1947: 124). The largest type appears to be particularly emaciated, as the body is thin, sunken, and bony posterior to the large head. The illustration by Günther (1868: Pl. 84, Fig. 6) is evidently based on BM 1864.1.26.187C, since the drawings of *Profundulus* he presented are natural size and this specimen (55 mm. long) agrees very closely with the one figured.

I find a definite trace of the deep brown spotting characteristic of *punctatus* in the 24 topotypes taken by Eisen, as well as in the three types and the one nontype. Furthermore, I believe that this species was introduced into Lake Atitlán at an early time. This is suggested by three lines of evi-

[6]Günther correctly listed three males, Regan four females, as types; the fourth specimen cannot be a type as it was not mentioned in the original description.

dence: (1) *Profundulus* is a stream fish – e.g., it does not live in Lake Amatitlán, to which it has ready access; (2) priests, and probably natives before or after them, are known to have made early transplants, as of *Cichlasoma guttulatum* (Günther) into Lake Amatitlán in 1549 (Kelsey and Osborne,

TABLE II

COMPARISON BETWEEN THE TWO SPECIES GROUPS OF *PROFUNDULUS*

Character	*Punctatus* Group (*P. punctatus, P. guatemalensis*)	*Labialis* Group (*P. labialis, P. candalarius, P. hildebrandi*)
Preorbital	Well scaled; narrower	Usually naked or with 1 or 2 isolated, embedded scales; broader
Coloration of adult (Pls. I-IX)	Dark, often with a lateral band and chainlike reticulations on sides, or with rich brown spots in longitudinal rows along sides onto caudal fin; humeral spot present	Light, without definite lateral band but with disrupted light markings and light spots on sides; no humeral spot
Caudal fin	Basal half or more densely scaled	Less than half of base densely scaled
Dorsolateral scales*	5	Predominantly 6, rarely 5, sometimes 7 (5 in *candalarius* and *hildebrandi*)
Scales in lateral series (Table XIV)	Usually 32-34 (31-35, 36 in 1)	Usually 35-38 (34-39†)
Vertebrae (Table XIV)	32 to 34, uncommonly 31 or 35 (36 in 1)	35 to 39, typically 36 to 38 (33-37 in *candalarius* and *hildebrandi*)
Lower jaw	Broad, heavy and protruding so that upper jaw is included	Like upper jaw and either equal in forward projection or included (except *hildebrandi*, which resembles *guatemalensis*)
Anal fin of adult female (Pls. II-III, V, VII-VIII)	Typically only moderately elongated, the anterior rays not greatly longer than the posterior ones	Typically much elongated (except in *candalarius*), the anterior rays much longer than the posterior ones
Dorsal origin	Over or in advance of anal origin	Slightly to distinctly behind anal origin
Rostral head pores of adults (Fig. 2A)	Undeveloped, represented only by pit organs	Usually developed, at least in part (sometimes obsolete in *candalarius*)

*Number of scale rows from middle of back to (but not including) lateral series.
†Except *P. candalarius* which usually has 34 (33-36).

1946: 229; also correspondence in 1949 with Mrs. Osborne), and several species are known to have been planted in Lake Atitlán in the past 50 years; and (3) the species reported by Günther (1866: 321-22) and by Meek (1908: 186, as *F. guatemalensis*) was not found by our party in 1946, but a *Profundulus (P. labialis)* was taken then in the stream at Panajachél, tributary to Lake Atitlán, and evidently represents a recent introduction. Indeed, it may be questioned whether Lake Atitlán has contained any native fishes since its origin. Of the eight species found in that basin in 1946, five were definitely stated to have been introduced, but *Profundulus labialis, Mollienesia sphenops*, and *Cichlasoma nigrofasciatum* were thought to be native.

Profundulus oaxacae is relegated to the synonymy of *P. punctatus* because, as pointed out by Meek (1902: 91, Pl. XX) and since confirmed by an examination of the type series, the bodies of many of the specimens show the typical (though now much faded) spotting of *punctatus*. The absence of such spotting on the few specimens previously seen led me (Miller, 1950: 27) to retain *oaxacae* as a full species. The supposedly distinguishing characters mentioned by Meek (1902: 91, Pl. XX) and by Hubbs (1924: 15) — a large head, more robust body, more anterior dorsal, larger scales, smaller size, and smaller eye — all fail to separate *oaxacae* specifically from *punctatus*. I therefore follow Regan (1906-8) in treating *oaxacae* as a synonym of *punctatus*.

The status of *Profundulus balsanus* Ahl is uncertain in two particulars: (1) whether it is a valid form and (2) whether the type specimens really came from the Río Balsas drainage. Recently (Miller, 1950: 28-29), I pointed out, after receiving advice from Dr. José Alvarez, the likelihood that the types really came from the Río Santa Catarina (item 3, Map 1), an independent Pacific tributary. The meristic characters and other features of *balsanus* cannot be determined from the two small, partly dried paratypes (UMMZ 157291) at hand. The only certain conclusion is that *balsanus* belongs to the *P. punctatus* species group. I, therefore, provisionally synonymize *balsanus* with *punctatus*.

Profundulus scapularis Fowler, described from Finca Mocá (Maps 2-3), Guatemala, has already been placed in the synonymy of *P. punctatus* (Miller, 1950: 27). Subsequent examination of the type series (ANSP 64137, 64138-47, 64242-70) fully confirms this action, for the nominal species agrees in all technical characters with *punctatus*, a species with which it was not compared. The material from El Zapote (Fowler, 1936: 522, Figs. 21-23), on a tributary of the Río Guacalate about eight airline miles northwest of Escuintla at an elevation of 2,500 feet, is *P. guatemalensis* (ANSP 64722-33); the specimens from Chimaltenango (Fowler, 1936: 524, Fig. 24), in the same drainage (Map 2) are also *P. guatemalensis* (USNM 134620 and UMMZ 166681).

A rather detailed synonymy of this species, correct except for the inclusion of *P. guatemalensis*, is given by Holly, Meinken, and Rachow (1938: 244).

Type. — A mature male, BM 1864.1.26.420, 77 mm. in standard length, secured by Salvin reportedly at Chiapám, on the Pacific Coast of Guatemala. Günther (1868: 381) described this locality as a coastal lagoon near the mouth of a river with water "almost salt" but varying with the season, and located it on his map (Pl. 63) near the present port of Champerico. According to Griscom (1932: 415), it lies one-half mile from Champerico (Map 2). If the specimen really came from Chiapám,[7] it must have been washed there during a heavy flood, for our rather extensive survey did not reveal *Profundulus punctatus* nearer than 15 to 18 miles from the coast or lower than about 300 feet above sea level. The habitat described for Chiapám is most atypical for *Profundulus*.

Variation. — Although *Profundulus punctatus* has the greatest range of any species of the genus (southern México nearly to El Salvador, from about 300 to 5,200 feet), it is relatively uncommon in collections and only 897 specimens (428 collected by me) were available for study. These show great variation in meristic characters between adjacent as well as distant populations (Tables IV-VI). Certain character trends (Table III) are evident, however. Thus, those populations inhabiting the region about the Isthmus of Tehuantepec and westward (Map 1) have 31 or 32 scales along the side and 31 to 33 vertebrae, in contrast to a greater average number elsewhere. They also average somewhat fewer in number of anal and caudal rays but have more scales around the body than do more southerly samples. The differences are not of sufficient magnitude or consistency, however, to permit nomenclatorial recognition; moreover, the populations within this region vary considerably in other meristic characters and in general body proportions and coloration. Thus the sample from the Río Verde at Oaxaca (item 4, Map 2), representing the types of *Fundulus oaxacae*, is readily distinguishable from a sample (UMMZ 108595) from the Río Papagayo near Acapulco (item 2, Map 1). The Verde specimens have a smaller eye, longer head, and attain a smaller maximum size, and most of them show the dark body spotting of *punctatus*. The Papagayo specimens differ most obviously in the apparent absence of such spotting, but whether these markings failed to develop in this sample, have faded, or the Papagayo stock lacks the spots, remains to be determined. The scales around the body are dominantly 28 in the Papagayo sample as contrasted with typically 30 in the Verde material (Table VI). This is a difficult count, however, subject to error due to regenerated scales; about one-third of the counts for the Río Verde lot are questionable. The Papagayo series usually has 11 or 12 dorsal rays and 20 or 21 caudal rays, whereas the Verde sample typically has 12 dorsal and 19 or 20 caudal rays (Tables IV-V). Certain meristic characters vary similarly with latitude and elevation; thus character trends from north to south are often matched by the same trend operating from high to low elevations. Other characters do not appear to be correlated with latitude or elevation (Tables IV-VI).

Such variations characterize the many populations of this species, of *P. guatemalensis*, and of *P. labialis*, and seem to defy arrangement in an orderly sequence of sufficient magnitude and consistency to enable the recognition of worthy taxonomic units. There are, however, some exceptional populations which constitute borderline cases. One of the most distinctive of these is the sample collected by M. W. Stirling at Piedra Parada, Chiapas (Map 1), 22 miles westward from Tuxtla Gutiérrez and about 12 miles north of

[7] Early collectors, such as Godman and Salvin, typically worked from a base camp, and specimens secured at considerable distances from such localities often bore the base-camp label (see also Goldman, 1951: 193).

TABLE III

CHARACTER TRENDS IN POPULATIONS OF *PROFUNDULUS PUNCTATUS*

Usual value is given, followed by range in parentheses.
Data from Tables V, VI, and XIV; for localities, see Maps 1 and 2.

Character	Isthmus of Tehuantepec and Westward*	Eastward from Tehuantepec	Piedra Parada, Chiapas	Finca La Paz, Guatemala
Anal rays	13 or 14 (12-15)	13 or 14† (11-16)	15 or 16 (14-17)	14 or 15 (14-16)
Caudal rays	19 to 21 (18-23)	19 to 21‡ (18-23)	22 (21-24)	22 (20-24)
Lateral scales	31 or 32 (31-33)	32 or 33 (31-34)	33 or 34 (33-34)	34 (33-35)
Vertebrae	31 or 32 (31-33)	32 or, usually, 33 (32-34)	33 or 34 (33-34)	33 or, usually, 34 (33-34)
Scales around body	28 or 30 (28-30)	26 or 28 (26-30)	26 (26-28)	28 (26-30)

*Not including the two paratypes of *P. balsanus*.

†14 or 15 in UMMZ 166668, Río Montebonito, a Pacific tributary 15 mi. N of Arriaga, Chiapas.

‡21 or 22 in UMMZ 158447, Finca Santo Tomás near southeastern arm of Lake Atitlán, Guatemala (seven specimens; see Map 3).

Ocozocoautla (see Smith, 1946). The arid valley in which the little town lies comprises a limestone plateau, overlain by sand, open and grassy, with small clumps of trees along the small stream. The elevation is about 1,100 meters (3,630 feet). During the dry season the stream is only about one-half mile long and sinks into the sandy plain; in the wet season it is five miles long and fans out onto the plain, but even then it maintains no direct connection with a major drainage though it drains toward the Atlantic. In addition to *P. punctatus* the stream is inhabited by an Atlantic species, *Pseudoxiphophorus bimaculatus* (Heckel), which also shows local differentiation. These fishes are effectively cut off from other fish populations. An examination of Tables IV to VI shows that the Piedra Parada sample has an increased number of dorsal, anal, and caudal rays and that the lateral scales and vertebrae also average greater than those of most populations of *P. punctatus*. The scales around the body, if these were determined with reasonable accuracy, do not reflect this increase, however. Despite these differences and an indication that this sample has a shorter head than other populations of *punctatus* measured, the overlap in counts and the general aspect of fluctuating variation in this and other species of *Profundulus* caution me against giving nomenclatorial recognition to the population at this time. Another factor contributed to this decision. The collector, an anthropologist, could only obtain the local alcoholic beverage, *aguardiente*, in which to preserve his catch, with the result that the specimens are soft and limp and the accuracy of the scale counts and measurements is subject to greater error than in well-preserved samples.

Another population that might be named (and probably would have been if only Guatemalan material had been studied) is that at Finca La Paz, in the Department of San Marcos, Guatemala. This locality is on a tributary

TABLE IV

DORSAL AND PECTORAL FIN-RAY COUNTS IN *PROFUNDULUS PUNCTATUS*

Within each category, localities are arranged from SE to NW (see Maps 1-3), with number of collections in parentheses.

Locality	Dorsal Rays								Pectoral Rays						
	10	11	12	13	14	15	No.	Ave.	16	17	18	19	20	No.	Ave.
GUATEMALA															
Coastal Plain and Piedmont															
SE to La Democracia (5)	11	61	32	2	..	..	106	11.23	5	71	107	29	..	212	17.75
Patulul to 91°30′ (4)	..	13	42	15	..	..	70	12.03	..	4	48	76	8	136	18.65
92° to Malacatán (2)	..	7	22	2	..	..	31	11.84	..	9	43	10	..	62	18.02
S Slopes of Cordillera															
Yepocapa and Rosario (2)	1	16	26	13	1	..	57	11.95	..	5	42	26	3	76	18.35
Lake Atitlán* (2)	..	4	16	6	2	..	28	12.21	2	7	28	13	5	55	18.22
Finca Mocá† (2)	..	11	22	4	..	..	37	11.81	..	2	42	26	4	74	18.43
Finca La Paz (1)	..	..	8	16	6	..	30	12.93	..	1	20	32	7	60	18.75
MEXICO															
Coastal Plain															
Escuintla to Arriaga (5)	..	5	7	1	..	..	13	11.69	..	3	13	6	..	22	18.14
Río Tehuantepec (3)	..	1	9	5	1	1	17	12.53	..	8	15	5	..	28	17.89
Río Papagayo (1)	..	14	15	1	..	..	30	11.57	1	22	28	9	..	60	17.75
Slopes and Highlands															
Río Montebonito (1)	..	..	7	18	2	..	27	12.81	..	16	30	6	..	52	17.81
Ortis Rubio to Chiapa (4)	..	..	6	6	2	..	14	12.71	..	1	18	7	..	26	18.23
Piedra Parada (1)	..	..	3	22	9	..	34	13.18	..	7	56	3	..	66	17.94
Río Coatzacoalcos (1)	..	..	3	5	..	..	8	12.63	..	1	6	5	..	12	18.33
Río Verde, Oaxaca‡ (1)	1	8	22	8	..	..	39	11.95	4	28	32	2	..	66	17.48

*Including the types of *P. pachycephalus*.
†Topotypes of *P. scapularis*; also seven specimens from S of San Lucas (UMMZ 158447).
‡Paratypes of *P. oaxacae*.

of the Río Naranjo, 19 airline miles due west of Quetzaltenango, at an elevation of about 1,200 meters or 3,930 feet (Map 2). This population is distinguished principally by an increased number of scales and vertebrae, both of which typically number 34 (Table III). It also has greater average values for other counts than do most populations but there is wide overlap in the number of dorsal, anal, and caudal fin rays with those of some of the other samples (Tables IV-VI). The number of lateral scales and vertebrae overlaps that of the Piedra Parada series too greatly to permit subspecific separation on that basis.

The collection from Río Montebonito (Map 1), a Pacific tributary 15 miles north of Arriaga on the road to Tuxtla, Chiapas, indicates the type of variation one can find within a single stream. This form approaches that from Piedra Parada, except in number of caudal rays, lateral scales, and vertebrae, and it is likewise similar to the sample from Finca La Paz in much the same counts (Tables IV-VI). In a collection taken lower down on the coastal plain, and in part in the same stream, the dorsal and anal rays average fewer, although most of the other counts seem to agree, considering the small size of the samples.

I conclude that there is too much random variation associated with too little geographic consistency to justify nomenclatorial recognition of any of the scattered populations of *P. punctatus*.

Range. — On the Pacific slope from the Río Papagayo in Guerrero, southern México, to the vicinity of Chiquimulilla, Department of Santa Rosa, southern Guatemala. On the Atlantic slope, from the Isthmus of Tehuantepec (Río Coatzacoalcos drainage; UMMZ 161522), Oaxaca, to the basin of the Río de Chiapa, Chiapas, México (see Map 1).

TABLE V

ANAL AND CAUDAL FIN-RAY COUNTS IN *PROFUNDULUS PUNCTATUS*

Within each category, localities are arranged from SE to NW (see Maps 1-3), with number of collections in parentheses.

Locality	Anal Rays									Caudal Rays								
	11	12	13	14	15	16	17	No.	Ave.	18	19	20	21	22	23	24	No.	Ave.
GUATEMALA																		
Coastal Plain and Piedmont																		
SE to La Democracia (5)	..	9	60	33	4	..	..	106	13.30	2	26	40	27	9	2	..	106	20.20
Patulul to 91° 30′ (4) . .	..	1	12	40	16	1	..	70	14.06	..	7	19	29	10	1	..	66	20.68
92° to Malacatán (2) . .	..	..	10	15	6	..	..	31	13.87	..	5	12	8	4	1	..	30	20.47
S Slopes of Cordillera																		
Yepocapa and Rosario (2).	..	2	11	32	11	1	..	57	13.96	..	2	4	16	8	4	..	34	21.23
Lake Atitlán*(2)	1	4	10	12	1	..	..	28	13.29	..	3	12	6	1	2	..	24	20.46
Finca Mocá† (2)	..	3	10	20	4	..	..	37	13.67	..	2	10	16	5	3	..	36	20.92
Finca La Paz (1). . . .	..	..	..	13	15	2	..	30	14.63	..	..	1	6	13	5	5	30	22.23
MEXICO																		
Coastal Plain																		
Escuintla to Arriaga (5)	..	..	7	4	2	..	..	13	13.61	..	..	2	5	2	..	..	9	21.00
Río Tehuantepec (3) . .	..	..	4	11	2	..	..	17	13.88	..	2	3	2	1	1	..	9	20.55
Río Papagayo (1). . . .	..	..	19	11	..	..	..	30	13.37	..	2	12	11	3	..	..	28	20.53
Slopes and Highlands																		
Río Montebonito (1) . .	..	..	..	13	15	1	..	29	14.59	..	..	3	17	4	1	..	25	21.12
Ortis Rubio to Chiapa (4).	..	..	3	6	4	1	..	14	14.21	..	2	2	5	..	..	..	9	20.33
Piedra Parada (1) . . .	..	..	..	1	12	17	4	34	15.71	..	..	..	1	23	8	2	34	22.32
Río Coatzacoalcos (1) .	..	..	..	2	6	..	..	8	14.75	..	..	1	2	..	..	..	3	20.67
Río Verde, Oaxaca‡(1).	..	1	17	17	4	..	..	39	13.61	5	15	14	5	..	..	..	39	19.49

*Including the types of *P. pachycephalus*.
†Topotypes of *P. scapularis;* also seven specimens from S of San Lucas (UMMZ 158447).
‡Paratypes of *P. oaxacae*.

Regan (1906-8: 78) recorded this species from San Domingo de Gúzman, México, collected by A. C. Buller. There are a number of places in México bearing this name, but this one is in the Atlantic drainage because Regan described *Pseudoxiphophorus bimaculatus taeniatus* and *Heros callolepis* from the same locality. The latter species belongs to the *Thorichthys* group, which comprises cichlids confined to the Atlantic drainage. What I judge to be the proper location is shown as "S. Domingo" on the map "Carta de Reconocimiento del Istmo de Tehuantepec, Canal Interoceano," dated 1871 (scale 1:500,000), just west of Petapa on an upper tributary of the Río Coatzacoalcos (Map 1). Goldman (1951: 224) described the same locality under the name Santo Domingo, elevation 900 feet. The locality is in Oaxaca, where Dr. Buller is known to have collected in the 1890's (Regan, 1906-8: vii).

TABLE VI

SCALE COUNTS IN *PROFUNDULUS PUNCTATUS*

Within each category, localities are arranged from SE to NW (see Maps 1-3), with number of collections in parentheses.

Locality	Lateral Scales							Scales Around Body								
	31	32	33	34	35	No.	Ave.	24	25	26	27	28	29	30	No.	Ave.
GUATEMALA																
Coastal Plain and Piedmont																
SE to La Democracia (5) . .	9	49	41	..	..	99	32.32	2	2	76	3	16	..	..	99	26.29
Patulul to 91°30′ (4).	..	20	35	3	..	58	32.71	..	..	29	7	22	..	..	58	26.88
92° to Malacatán (2)	..	8	20	3	..	31	32.84	..	..	21	2	8	..	..	31	26.58
S Slopes of Cordillera																
Yepocapa and Rosario (2) . .	..	2	19	7	..	28	33.18	..	..	6	1	7	..	..	14	27.07
Lake Atitlán* (2)	1	9	13	3	..	26	32.69	..	..	2	2	10	..	..	14	27.57
Finca Mocá† (2)	..	20	16	1	..	37	32.49	..	1	28	2	5	..	..	36	26.31
Finca La Paz (1).	..	..	6	23	1	30	33.83	..	..	7	3	16	3	1	30	27.60
MEXICO																
Coastal Plain																
Escuintla to Arriaga (5) . . .	..	8	5	..	..	13	32.38	..	..	10	2	1	..	..	13	26.31
Río Tehuantepec (3)	5	6	..	..	..	11	31.55	..	..	..	..	3	..	2	5	28.80
Río Papagayo (1).	16	14	..	..	..	30	31.47	..	..	..	..	20	3	7	30	28.57
Slopes and Highlands																
Río Montebonito (1)	..	23	5	..	..	28	32.18	..	..	12	2	11	1	1	27	27.15
Ortis Rubio to Chiapa (4) . .	2	7	7	1	..	17	32.41	..	..	7	..	1	..	..	8	26.25
Piedra Parada (1)	..	..	18	13	..	31	33.42	..	..	19	1	3	..	..	23	26.30
Río Coatzacoalcos (1)	5	3	..	..	..	8	31.37	..	..	2	..	2	..	..	4	27.00
Río Verde, Oaxaca‡ (1) . . .	17	20	..	..	..	37	31.54	..	..	1	..	1	3	20	25	29.64

*Including the types of *P. pachycephalus*.
†Topotypes of *P. scapularis;* also seven specimens from S of San Lucas (UMMZ 158447).
‡Paratypes of *P. oaxacae*.

Profundulus guatemalensis (Günther)

Pls. III – IV

Fundulus guatemalensis. — Günther, 1866: 321 (orig. descr.; Río Guacalate,[8] Lake Dueñas, and L. Amatitlán, Guatemala, and "Western Ecuador"); 1868: 482-83, Pl. 84, Figs. 3 and 4 (redescr. with figs.). Regan, 1906-8: 78 (synonym of *F. punctatus*). Meek, 1907: 136-37 (L. Amatitlán and L. Atitlán).

Zoogoneticus guatemalensis. — Meek, 1902: 94 (name only).

Profundulus guatemalensis. — Hubbs, 1924: 13 (provisional synonym of *punctatus*). Miller, 1950: 27-28 (recognized as distinct from *punctatus*).

Profundulus punctatus (misidentification). — Hildebrand, 1925: 253-54 (Río Molino near Ahuachapán; range). Fowler, 1936: 520-24, Fig. 24 (Río de las Vacas, Antigua, and outlet L. Amatitlán).

Profundulus scapularis. — Fowler, 1936: 522, 524, Figs. 21-24 (in part, not types; El Zapote and Chimaltenango material only).

Fundulus parvipinnis (misidentification). — Garman, 1895: 100 (in part; *guatemalensis* in synonymy).

The reasons for recognizing *guatemalensis* as a full species have been discussed under the preceding account. *P. guatemalensis* differs chiefly and most conspicuously from *P. punctatus* in lacking the rich brown spotting on the body and caudal fin.

[8]Type locality, as herein restricted (see text).

Lectotype. — Three of the four localities from which this species was described are either grossly in error (e.g., Ecuador) or possibly not exact (e.g., Lake Amatitlán, Lake Dueñas; more plausibly from streams entering or leaving these lakes). The Río Guacalate, however, is still inhabited by *P. guatemalensis*, and available material well represents the species and compares favorably with the single specimen recorded by Günther from this stream. I thereby restrict the type locality to the Río Guacalate by selecting as lectotype BM No. 1864.1.26.364, a nuptial male (Pl. II, Fig. A), 64 mm. in standard length, collected by Salvin. Type locality: Río Guacalate (Pacific drainage), in the highlands of Guatemala, probably near Dueñas which is five miles southwest of Antigua. According to Günther (1868: 380), the fishes from this river "were obtained about 3500 feet above the sea, where the river is still quite a torrent." A series of specimens collected by me on March 27, 1946, from the Río Guacalate about one mile below Antigua, may be considered topotypic; these have been deposited in the U. S. National Museum (134619) and the University of Michigan Museum of Zoology (166680).

The following data are recorded for the lectotype: Dorsal 12 (first ray unbranched), anal 15 (first two rays unbranched), pectorals 19-19, pelvics 6-6, caudal 23; scales in lateral series 32, before dorsal 24 (19 + 5), around caudal peduncle 22 (10 + 12), and around body 28 (?); vertebrae 32; 18 gillrakers on left side of first arch.

Variation. — Variation in this species is not so marked as it is in *punctatus* and *labialis* — perhaps a reflection of its smaller range and of the less contrasting environmental factors. The dorsal rays (Table VII) average greater in the Atlantic populations from the Río Motagua and Río Negro basins (12.77 to 13.42 in contrast to 11.39 to 12.12 elsewhere), and the lateral scales (Table IX) and vertebrae are also more numerous in these populations, but are closely approached by the samples from the Río Lempa near Esquipulas, Guatemala, and from Intibucá, Honduras. The greatest average is for the populations from a tributary of the Motagua near San José de Pinula, southeast of Guatemala City (Map 2). This race lives at a higher elevation (about 5,300 to 6,500 feet) than any other sample of *guatemalensis* obtained. Its scale counts, however, overlap those from elsewhere in the Motagua and Negro basins, and from the Río Lempa, to such an extent that nomenclatorial recognition of the Pinula stock seems unwise. The body shape, proportions, and coloration of the samples between and within these drainages, show marked variations but little geographic consistency except that the Negro specimens lack the chainlike, reticulate pattern of the posterior sides that is typically (but not consistently) developed in populations of *guatemalensis* elsewhere.

A distinctive looking sample of *P. guatemalensis* was secured in Laguna del Pino (about 3,400 feet), approximately 30 miles southward from Guatemala City and just east of the Pan-American Highway (Map 2); however, most, and perhaps all, of its extreme characters may represent, largely or solely, an environmental response. In the rainy season this lake evidently overflows into the Río Aguacapa, as evidenced by a well-defined outlet channel northwest of the lake. It is assumed that *Profundulus* gains access to the lake at such times and is then trapped after the waters recede. This

TABLE VII

DORSAL AND PECTORAL FIN-RAY COUNTS IN *PROFUNDULUS GUATEMALENSIS*

Figures in parentheses after localities indicate the number of collections.

Locality*	Dorsal Rays								Pectoral Rays							
	10	11	12	13	14	15	No.	Ave.	16	17	18	19	20	21	No.	Ave.
PACIFIC																
Río Lempa Basin																
Intibucá, Honduras (1) . . .	..	..	..	3	..	1	4	13.50	..	..	6	1	..	..	7	18.14
Near Esquipulas (1)	2	12	20	6	..	..	40	11.75	3	46	33	..	..	..	82	17.37
Río de Paz Basin																
Ahuachapán, El Salvador (1)	..	6	12	1	..	..	19	11.74	..	1	3	24	..	..	28	18.82
Guatemala (3)	1	13	27	10	3	..	54	12.02	..	23	52	26	7	..	108	18.16
Río de los Esclavos Basin																
Cuilapa and above (6) . . .	4	50	66	10	..	..	130	11.63	..	6	85	110	22	..	223	18.66
Below Cuilapa (5)	2	27	37	8	..	..	74	11.69	..	1	23	78	34	..	136	19.07
Interior Drainage																
Lake Ayarza (1)	3	11	10	5	..	..	29	11.59	..	2	10	20	6	..	38	18.79
Río Aguacapa Basin																
Laguna del Pino (1)	1	20	10	2	..	..	33	11.39	3	35	28	..	..	..	66	17.38
Other localities (3)	..	19	46	24	..	1	90	12.09	..	5	89	79	4	..	177	18.46
Río Michatoya Basin																
Amatitlán† and above (5). .	1	15	45	10	2	..	73	11.96	2	4	50	73	13	4	146	18.71
Palín (1)	..	8	11	1	..	..	20	11.65	..	..	1	29	10	..	40	19.23
Below Palín (2)	..	11	35	10	4	..	60	12.12	..	3	26	81	10	..	120	18.82
Río Guacalate Basin																
Near Antigua (2)	2	8	31	15	3	..	59	12.15	..	8	42	56	14	..	120	18.63
Apocentos (1)	..	3	23	3	1	..	30	12.07	..	1	15	37	7	..	60	18.83
L. Dueñas‡ (1)	..	8	10	..	..	..	18	11.55	..	2	22	11	1	..	36	18.31
ATLANTIC																
Río Motagua Basin																
San José Pinula (2)	..	..	6	11	9	5	31	13.42	..	5	33	17	5	1	61	18.41
Other localities (8)	..	5	63	71	30	2	171	12.77	1	31	165	106	6	..	309	18.27
Río Negro Basin																
Three localities	..	..	14	43	22	1	80	13.13	..	14	64	74	8	..	160	18.47

*All localities are in Guatemala except as noted.
†Includes six paratypes of *P. guatemalensis*.
‡Paratypes of *P. guatemalensis*.

assumption is based upon (1) the avoidance of lakes by this genus; (2) the prevalence of regenerated scales on the specimens, which it does not seem logical to expect in a permanent, lacustrine population; (3) the relative scarcity of the genus in Laguna del Pino, for it was taken only at the northwest end, near the outlet; and (4) the emaciated condition of many of the fish. Moreover, on June 18, 1946 (about two and one-half months after our sample was collected), Sr. Fernando Barneond, field associate of the Guatemalan Department of Game and Fish, found many *Profundulus* dying along the northwestern shore of this lake. Laguna del Pino is shallow (not over six to seven feet deep in the upper basin), has a continuous marginal bed of cattails and bulrush (*Typha* and *Scirpus*), and a heavy growth of microscopic plants and animals during the dry season. On March 31, 1946, the turbidity was 55 (on U.S.G.S. meter) in water over a bottom of thick, fine mud, and *Profundulus* was secured only by vigorous and repeated seining back under rather dense vegetation, where the temperature was noticeably cooler than it was in the more open waters. A review of the ecological requirements of *Profundulus* supports the view that this population was living under atypical, unfavorable conditions. The meristic characters of this sample average significantly fewer than in any other stock of *guatemalensis* sampled, although it is closely approached in number of anal rays by the Guatemalan sample from the Río Lempa (Tables VII-IX).

TABLE VIII

ANAL AND CAUDAL FIN-RAY COUNTS IN *PROFUNDULUS GUATEMALENSIS*

Figures in parentheses after localities indicate the number of collections.

Locality*	Anal Rays								Caudal Rays									
	12	13	14	15	16	17	No.	Ave.	18	19	20	21	22	23	24	25	No.	Ave.
PACIFIC																		
Río Lempa Basin																		
Intibucá, Honduras (1)	..	..	..	4	..	..	4	15.00	..	..	..	2	1	..	..	..	3	21.33
Near Esquipulas (1) .	5	19	14	3	..	..	41	13.37	4	4	26	6	..	..	..	..	40	19.85
Río de Paz Basin																		
Ahuachapán, El Salvador (1).	..	3	11	5	..	..	19	14.11	..	1	..	6	6	2	3	..	18	21.94
Guatemala (3)	5	10	31	7	1	..	54	13.80	..	..	9	19	18	6	1	..	53	21.45
Río de los Esclavos Basin																		
Cuilapa and above (6).	5	47	62	15	1	..	130	13.69	..	5	13	32	33	16	..	1	100	21.46
Below Cuilapa (5) . .	..	13	43	17	1	..	74	14.08	1	4	11	31	16	3	1	..	67	21.04
Interior Drainage																		
Lake Ayarza (1) . . .	..	..	14	11	5	..	30	14.70	..	1	2	1	..	..	..	..	4	20.00
Río Aguacapa Basin																		
Laguna del Pino (1) .	..	22	8	3	..	..	33	13.42	3	..	8	12	7	2	1	..	33	20.91
Other localities (3). .	3	41	41	5	..	..	90	13.53	..	3	9	42	24	9	2	1	90	21.41
Río Michatoya Basin																		
Amatitlán† and above (5)	1	14	38	15	5	..	73	14.12	..	2	1	35	16	16	2	1	73	21.73
Palín (1)	..	1	13	5	1	..	20	14.30	..	1	..	6	5	6	1	1	20	22.10
Below Palín (2). . . .	..	3	26	29	2	..	60	14.50	..	..	2	13	15	19	9	2	60	22.43
Río Guacalate Basin																		
Near Antigua (2) . . .	1	9	31	17	1	1	60	14.18	..	..	6	26	23	4	1	..	60	21.47
Apocentos (1).	..	6	21	3	..	..	30	13.90	..	..	4	14	8	4	..	..	30	21.40
L. Dueñas‡ (1)	..	5	10	3	..	..	18	13.89	..	..	1	11	2	4	..	..	18	21.50
ATLANTIC																		
Río Motagua Basin																		
San José Pinula (2). .	..	3	8	12	7	1	31	14.84	1	6	8	11	5	..	..	..	31	20.42
Other localities (8). .	1	20	82	61	7	..	171	14.31	4	17	80	25	21	2	..	..	149	20.32
Río Negro Basin																		
Three localities . . .	..	22	47	11	..	..	80	13.86	..	1	12	25	39	3	..	..	80	21.39

*All localities are in Guatemala except as noted.
†Includes six paratypes of *P. guatemalensis*.
‡Paratypes of *P. guatemalensis*.

The close resemblance in meristic characters between the Pino sample and *P. punctatus* is not thought to indicate particularly close relationship, since none of the specimens shows the brown spotting so typical of *punctatus* and that species was not secured at three other highland stations along the Río Aguacapa, the flood-stage outlet of Laguna del Pino. The fewer fin rays and scales that characterize the Pino sample are believed to be, at least in some degree, a local environmental response.

The sample from Lake Ayarza (Map 2), a caldera lake about 34 airline miles east of Amatitlán, met with misfortune when packed out on the back of a mule and nearly all of the fins were broken and the specimens otherwise rendered unfit for critical study. This unproductive, deep lake (756 feet, maximum depth sounded), without inlet or visible outlet, is approximately 4,800 feet above sea level. It is largely rimmed by the steep walls of the old crater, but near the north end at a small beach there is a low pass that was estimated to be 115 feet above the lake. The depth off the beach increases very abruptly so that the water is 30 or more feet deep only 20 to 30 feet from shore, and there is almost a vertical drop elsewhere.

A local fisherman, who had lived over 40 years by the lake, told us that *Profundulus guatemalensis,* the only fish we obtained, has always been in the lake. If it is native, it evidently gained access to the lake when its level was high enough to spill water over the pass. We noted no evidence for such an outlet or for a higher lake stage. On the other hand, it is known that attempts have been made to introduce cichlids and perhaps other large fishes into this lake, and it is reasonable to suppose that *Profundulus* was stocked at an early time. During our visit, on May 11, 1947, we were told that the latest plantings had been made six weeks earlier when cichlids were brought in cans from Lake Amatitlán. The fisherman told us that all such attempted plants have evidently failed. The lake abounds with frogs and crabs; the latter form the staple diet of the small native population.

The specimens from Lake Ayarza that were countable show no striking variation from most of the other populations of *guatemalensis.* X-ray photographs demonstrate that the number of vertebrae (almost perfectly correlated with the lateral-scale counts) agrees very closely with that of other samples from the Highlands. The few intact individuals look like most of the samples of this species, which may or may not support the suggestion that *Profundulus* is not native to the lake.

Profundulus guatemalensis and *P. punctatus* have been found in the same drainages only in the Río Michatoya, outlet of Lake Amatitlán, and in the Río Guacalate, which rises near Antigua, Guatemala. In neither of these streams, however, have they been collected together. My lowermost record for *guatemalensis* in the Michatoya is from a swift-flowing tributary approximately three and one-half miles north of Escuintla, at an elevation of about 1,750 feet, on the road to Palín. The uppermost collection of *punctatus* in the Michatoya is from a small tributary about seven miles southeast of Escuintla, elevation estimated to be 700 feet, on the main road to Chiquimulilla (Map 2). Escuintla is about 1,250 feet above sea level. Each of these samples is readily identifiable to species with no evidence of any closer approach in characters than other, more widely separated, samples of the two species.

In the Río Guacalate basin time did not permit an intermittent sampling of the drainage from the upper part down to the edge of the coastal plain. *P. guatemalensis* was abundant in the Highlands, above and below Antigua (4,884 feet), and probably occurs downstream at least as far as Alotenango (about 3,800 feet). *P. punctatus* has been taken on the coastal plain between Mixtán and Santa Maria (about 500 feet) and in the Río Aceituno (about 600 feet), 8.2 miles west of Escuintla. The Río Aceituno is a tributary of the Río Achiguate, which in turn flows into the Guacalate below Masagua. Under the name *Profundulus scapularis, P. guatemalensis* was reported by Fowler (1936: 522 from a tributary of the Achiguate at El Zapote, elevation 2,500 feet, about five and one-half airline miles north of the Aceituno station.

Although *P. punctatus* has been found in the basin of the Río Chiquimulilla, near Chiquimulilla, it is not known from the Río de los Esclavos, just to the

TABLE IX

SCALE COUNTS IN *PROFUNDULUS GUATEMALENSIS*

Figures in parentheses after localities indicate the number of collections.

Locality*	Lateral Scales								Scales Around Body							
	31	32	33	34	35	36	No.	Ave.	-26	27	28	29	30	31	No.	Ave.
PACIFIC																
Río Lempa Basin																
Intibucá, Honduras (1) . . .	..	..	1	3	..	..	4	33.75	..	..	2	..	..	..	2	28.00
Near Esquipulas (1)	..	..	12	26	3	..	41	33.78	13	6	21	..	1	..	41	27.27
Río de Paz Basin																
Ahuachapán, El Salvador (1)	..	9	6	..	..	..	15	32.40	1	2	10	..	..	..	13	27.69
Guatemala (3)	..	12	36	6	..	..	54	32.89	4	3	44	1	1	..	53	27.85
Río de los Esclavos Basin																
Cuilapa and above (6) . . .	..	6	69	32	1	..	108	33.26	5	1	84	4	8	1	103	28.12
Below Cuilapa (5)	1	22	46	3	..	..	72	32.71	25	8	31	1	2	..	67	27.21
Interior Drainage																
Lake Ayarza (1)	..	1	15	5	..	..	21	33.19	1	..	7	1	4	..	13	28.54
Río Aguacapa Basin																
Laguna del Pino (1)	6	23	4	..	..	..	33	31.94	9	..	..	..	..	..	9	26.00
Other localities (3).	..	24	62	4	..	..	90	32.78	19	7	63	..	..	..	89	27.49
Río Michatoya Basin																
Amatitlán† and above (5). .	..	41	30	2	..	..	73	32.47	3	..	30	..	3	..	36	28.00
Palín (1)	..	18	2	..	..	..	20	32.10	6	1	13	..	..	..	20	27.35
Below Palín (2).	..	21	39	..	..	..	60	32.65	11	6	42	1	..	..	60	27.55
Río Guacalate Basin																
Near Antigua (2)	..	18	39	3	..	..	60	32.75	..	..	25	2	4	..	31	28.32
Apocentos (1)	..	7	21	2	..	..	30	32.83	..	..	19	2	9	..	30	28.67
L. Dueñas‡ (1)	1	8	8	..	..	..	17	32.41	..	..	3	..	..	..	3	28.00
ATLANTIC																
Río Motagua Basin																
San José Pinula (2).	..	..	3	20	7	1	31	34.19	8	2	17	3	..	..	30	27.50
Other localities (8).	1	18	54	90	3	..	166	33.46	9	2	66	6	9	1	93	28.07
Río Negro Basin																
Three localities	1	15	23	23	2	..	64	33.16	24	9	31	..	..	..	64	27.11

*All localities are in Guatemala except as noted.
†Includes six paratypes of *P. guatemalensis*.
‡Paratypes of *P. guatemalensis*.

east. The three samples of *Profundulus* taken in the Esclavos system between Chiquimulilla and Cuilapa are all clearly referable to *guatemalensis*. The two small collections (UMMZ 158449-50) from a tributary of the Esclavos near Finca La Gloria (480 meters), about eight airline miles ENE of Chiquimulilla, are inadequate, however, to demonstrate conclusively their reference to *guatemalensis* (p. 17). Only three large adults were obtained, and these had died before they were preserved. They lack the brown spotting characteristic of *punctatus*, but well-preserved series from this area are needed to check this important character.

Consequently, since there is no evidence that *guatemalensis* and *punctatus* intergrade geographically or that an adequate sample of each form cannot be readily identified, and since each shows moderate to marked differentiation approaching the subspecies level, I regard them as allopatric species.

Range. — The range of this species, although including both Atlantic and Pacific streams, is more restricted than that of either *punctatus* or *labialis*. It occurs in Pacific streams from the upper (highland) part of the Río Guacalate and its westerly tributary, the Achiguate, Guatemala, to the upland tributaries of the Río Lempa at least as far eastward as the Department of

Intibucá, Honduras. The species is unknown from the Pacific coastal plain but is present on the Piedmont in the basins of the Río Michatoya and the Río Guacalate and, presumably, the Río de los Esclavos, Guatemala (Maps 1-2). In the Atlantic drainage it has been taken only in Guatemala: in the upper Río Motagua and in three tributaries of the Río Negro — Río Rabinal, Río San Jerónimo, and Río Carchelá (Map 2). Its occurrence in Lake Ayarza, Guatemala, may be the result of an introduction. Its presence in Lake Calderas, which lies above and south of Lake Amatitlán, Guatemala, is known to be the result of stocking from Lake Amatitlán.

The eight specimens from "Western Ecuador" (BM No. 1860.6.19. 16-23) collected by Fraser agree well with samples that represent highland populations of *guatemalensis* and are obviously mislabeled. The male and female of *guatemalensis* figured by Günther (1868: Pl. 84, Figs. 3 and 4) are evidently from this lot, as none of the other type specimens coincides in length or sex with the drawings.

A single specimen (UMMZ 113398) in poor condition, but evidently this species, was taken by Albert Greenberg in 1936 reportedly from a tributary of the Río Choluteca, Tegucigalpa, Honduras. A recent careful survey of this drainage (Carr and Giovannoli, 1950) failed to disclose any *Profundulus*, and hence I regard the locality as erroneous.

THE *LABIALIS* GROUP (SUBGENUS *TLALOC*)

The validity of the *labialis* species group is demonstrated by the distinguishing characters given in the key on page 16 and in the comparison with the *punctatus* species group (Table II, p. 19). The nearly naked preorbital, smaller scales, more numerous vertebrae, and coloration are the chief characters which differentiate this group. Three species (*labialis, candalarius,* and *hildebrandi*) are recognized and may be placed in a separate subgenus, *Tlaloc,* recently described as a full genus (see below). Two of these species, *P. labialis* and *P. candalarius,* are closely related, the latter clearly derived from *labialis* under geographic isolation. *P. hildebrandi* is believed to represent a much earlier stage of evolution of the *labialis* complex, probably close to the presumed common ancestor of both species groups. All but *P. labialis* are confined to the Atlantic drainage.

Profundulus labialis (Günther)

Pls. VII – VIII

Fundulus labialis. — Günther, 1866: 319-20 (orig. descr.; "Guatemala" [= Río Chixoy], Río San Jerónimo,[9] and Yzabal, Guatemala); 1868: 481, Pl. 84, Figs. 1-2 (redescr. with figs.). Regan, 1906-8: 78 (redescr. of orig. material).

Zoogoneticus labialis. — Meek, 1902: 94 (name only).

Profundulus labialis. — Hubbs, 1924: 15-16 (comparison with *P. candalarius*). Miller, 1950: 28 (characters).

Fundulus parvipinnis (misidentification). — Garman, 1895: 100 (in part; *labialis* in synonymy).

[9]Type locality as herein restricted (see text).

Profundulus punctatus (misidentification). — Fowler, 1936: 520-21, Figs. 11-20 (in part; specimens from Río Chajic, Tecpán, and from brooks near San Cristóbal and between San Cristóbal and Santa Cruz, Guatemala; latter are tributaries to Río Cahabón of the Río Polochic basin — see Map 2).

Tlaloc mexicanus. — Alvarez and Carranza, 1951: 40-42, Figs. 1-2 (orig. descr.; type loc., near Ocosingo, Chiapas, México).

Profundulus labialis is the only widespread species of this complex, and its range nearly surrounds that of the other two species.

Lectotype. — The original description of this species was based on specimens from the Río Negro or Chixoy (originally listed only as Guatemala), the Río San Jerónimo, and "Yzabal" or "Lake Yzabal," Guatemala (Günther, 1866: 320; Regan, 1906-8: 78). Because of the vagueness of the locality Río Chixoy and the absence of *Profundulus* at Izabal or in Lake Izabal, the type locality is herein restricted to the Río San Jerónimo at San Jerónimo. The lectotype is hereby designated as BM No. 1864.1.26.192A, a male 99 mm. in standard length, collected by Salvin in the Río San Jerónimo at or near San Jerónimo. This specimen is evidently the one figured by Günther (1868: Pl. 84, Fig. 1), as it is the only type specimen that agrees perfectly in length with that drawing. A radiograph of the lectotype is reproduced herein (Pl. II, Fig. C).

The following counts are recorded for the lectotype: dorsal 13 (first two rays unbranched), anal 14 (first two rays unbranched), pectorals 19-19, pelvics 5-6, caudal 21; scales in lateral series 37, predorsal scales 29 (24 + 5), scales around caudal peduncle 20, 6 scales between mid-line of back and lateral-series row (not countable entirely around body); vertebrae 37.

Variation. — *Profundulus labialis* rivals or exceeds *P. punctatus* in variability. As in that species the variations do not make geographic sense, and I can discover no logical arrangement of the samples that would warrant assigning names to any population or group of populations. The chief variability lies in certain body proportions and in meristic characters. Thus head length and width, mouth width, snout shape, eye size, and dorsal fin position fluctuate between populations from well-isolated drainages as well as between samples within a single basin. There is much variation also in coloration and body shape and in fin-ray and scale counts (Tables XI-XIII, Figs. 3-6). A brief discussion of variation in these populations follows (for localities, see Map 2).

Río Negro Basin. — The Río Negro, or Río Chixoy (Chisoy) as it is called below the great horseshoe bend south of Cobán, forms the uppermost part of the Río Usumacinta — the largest river in Central America (item 8, Map 1). Rising north of Totonicapán, Guatemala, the Negro flows northward toward Huehuetenango, swings abruptly eastward for nearly 70 miles, and then turns sharply northward on entering the gorge of the Chixoy. The Río Salamá (known in its headwater region as the Río San Jerónimo) enters from the south at this point. The volume of the Negro is swelled considerably by the Río San Juan, which gushes out of the mountain side at Aguacatán, about ten miles east of Huehuetenango. Below the horseshoe bend the fish fauna of the Río Negro (Chixoy) is little known. A collection made by L. C. Stuart near the mouth of a small tributary, northwest of Cobán (Hubbs, 1950: 10-11),

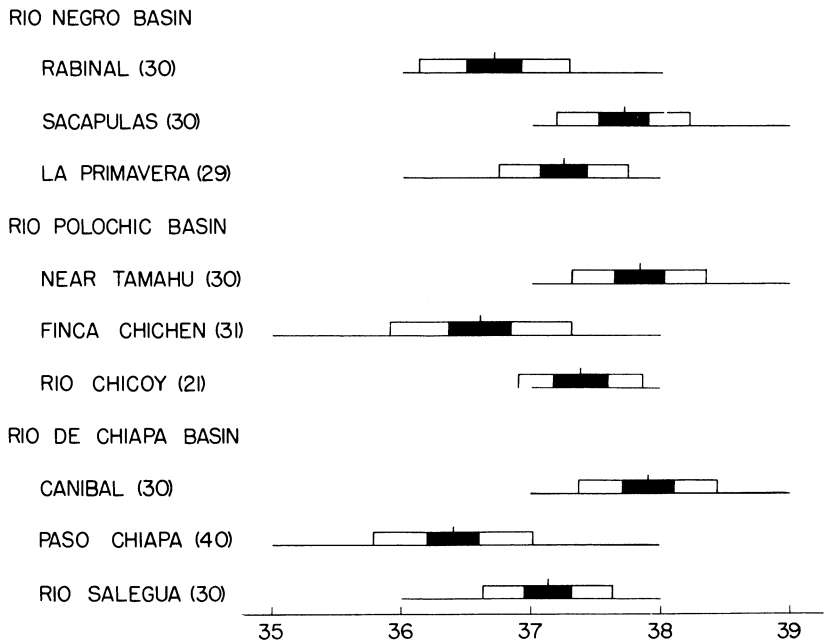


Fig. 3. Number of lateral scales in selected samples of *Profundulus labialis*. In this figure and the three that follow, range of variation is shown by the horizontal line; the mean (M) by the small vertical line. The blackened part of each bar represents two standard errors of the mean on either side of **M**. One-half of each black bar plus the white bar at either end outline one standard deviation on either side of **M**. The figure in the parentheses after each locality is the number of specimens.

revealed no *Profundulus*. From here, at an elevation of less than 1,000 feet, the river flows northward almost to the Mexican boundary, then turns westward and soon thereafter northward again to form the boundary between Guatemala and México. It eventually enters the Río Usumacinta which flows into the Gulf of México at the boundary of Tabasco and Campeche, México.

Adequate samples of ten populations from the Río Negro are available. Two collections from the extreme headwater area of the river are compared in Table X (see also Fig. 4) and demonstrate contrasts in characters which may be found in nearby populations. The collection from Río Momostenango was made about 2 miles north of Momostenango in a stream 6 to 12 feet wide and not over 3 feet deep, and that from Río Negro was seined later the same day 6 miles west-southwest of Santa Cruz Quiché (on the road to Totonicapán) in a stream 10 to 30 feet wide and no more than 3 feet deep. *Profundulus* was scarce at both localities, which are about 25 miles distant by water and lie at approximately the same elevation (6,700 ft.). The resemblances between the Momostenango collection and one from the Río Saleguá west of Huehuetenango (see Map 2) in the Río de Chiapa basin (p. 41), and between the Negro sample near Quiché and one from the Río Grande or Motagua (near Chichicastenango) in the Motagua basin (p. 38), strongly suggest former hydrographic connections between these now isolated basins (see section on Distribution and Origin).

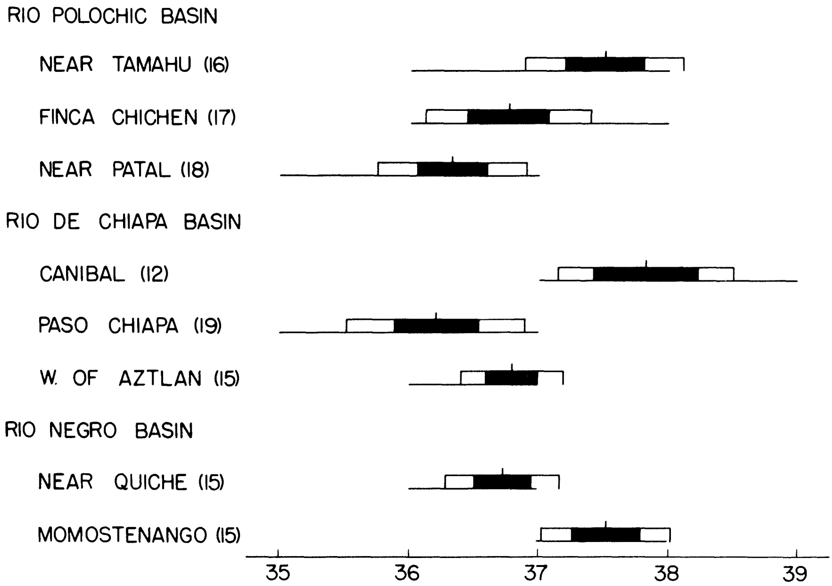


Fig. 4. Number of vertebrae in selected samples of *Profundulus labialis*. For explanation, see Fig. 3.

A large series of subtopotypes of *Profundulus labialis* from the Río Salamá (called Río San Jerónimo in its upper part) at Salamá, closely resembles several of the other Negro samples and is about average in meristic characters for all populations from the Negro basin (Tables XI-XIII). An attempt to obtain *P. labialis* at the type locality, San Jerónimo, yielded surprising results: 84 *Profundulus* were secured by using barbasco root, but only four of these are *labialis*, the remainder *guatemalensis*. Yet the latter species had never been taken heretofore in the Negro basin. Less than 10 miles downstream (at Salamá), however, several hauls of a large seine yielded only *P. labialis*.

A few selected examples of meristic variation in populations of *P. labialis* from the Río Negro and other basins are shown in Figures 3 and 4. It will be noted that extremes within a single drainage are matched by similar data for each of the other, independent river systems. Consequently, although samples within a drainage may diverge considerably in meristic as well as morphometric characters, at least one population in each basin closely resembles a population from a different system.

Thus, the collections of *Profundulus labialis* from the basin of the Río Negro comprise individual populations that vary in distinctiveness but lack a consistent character or set of characters by which they might be recognized nomenclatorially. Moreover, one race (from Río Carchelá) closely resembles some populations in the adjacent but well-isolated, Río Polochic drainage; another (from Río Momostenango) is like a sample (from Río Saleguá) in the separate basin of the Río de Chiapa; and still another race (Río Negro near Quiché) is rather similar to populations from a third major basin — that of the Río Motagua. For these reasons I refer all of these populations to *P. labialis*.

TABLE X

COMPARISON BETWEEN TWO NEARBY POPULATIONS OF *PROFUNDULUS LABIALIS* FROM THE RÍO NEGRO BASIN, GUATEMALA (see Map 3)

Character*	Río Momostenango III:31:1947 (6,700 ft.)	Río Negro III:31:1947 (6,700 ft.)
Dorsal rays	11 to 13, ave. 12.40	12 to 14, ave. 12.97
Caudal rays	20 to 22, ave. 21.13	20 to 22, ave. 21.73
Lateral scales	37 to 39, ave. 37.65	36 to 38, ave. 36.97
Vertebrae	37 or 38, ave. 37.53	36 or 37, ave. 36.73
Head into standard length† . .	3.5 to 3.9	3.45 to 3.6
Mouth	Narrower	Broader
Eye	Moderate	Slightly larger

*Data for first three characters taken from Tables XI-XIII.

†Stepped measurements based on seven specimens, 51 to 85 mm. long, from Río Momostenango, near Momostenango, and eight fish, 50 to 94 mm. long, from Río Negro, six mi. WSW of Santa Cruz Quiché. A 44 mm. fish from Momostenango yielded a ratio of 3.4.

Río Polochic Basin. – The Río Polochic (Map 2) and its major tributary, the Río Cahabón, rise in the cloud forest area south of Cobán. The Cahabón, called the Río Cobán in the headwater region, flows northward to Cobán and then turns abruptly eastward to join the Polochic eventually at Cahaboncillo, below Panzós. The Polochic flows due east from its source to Lake Izabal, the outlet of which (the Río Dulce) traverses a limestone gorge to the Atlantic.

Four samples, selected for extreme as well as intermediate expression of meristic characters, are compared graphically (Figs. 3-5). The specimens from Finca Pansamalá look like those from Finca Chichén, but the dorsal fin is more anterior and there is a striking difference in the number of dorsal rays (Fig. 5) as well as anal rays (Table XII). This numerical increase may have resulted, in part at least, from the small size of the sample. The Río Pansamalá, however, is isolated by a series of falls which are impassable for fish life in the rainy season; in the dry season, the falls section of the stream is dry (according to information from L. C. Stuart). A larger collection from this locality is needed to check the indication of a high number of dorsal and anal rays shown by the 12 available specimens. One sample from the Negro basin, taken in Río Carchelá, exhibits the long broad head, large eyes, and coloration that is generally developed in the Polochic populations.

Although we repeatedly attempted to secure *Profundulus* from the Río Polochic between La Tinta (about 330 feet), at the junction of the Río Panimá, and Tamahú (around 4,000 feet), the genus was not collected until just above Tamahú (Map 2); in the next five miles of the river it was abundant (and the only fish secured) and occurred to within three miles of the sharp divide (5,250 feet) that separates the Río Polochic from the Río Cobán (Map 2). In the Río Cahabón, it has not been taken or reported below about 4,100 feet. One of the original localities listed for this species is "Yzabal" (Günther, 1866: 320) or "Lake Yzabal" (Regan, 1906-8: 78), neither of which is more than 50 feet above sea level. During an eleven-day survey of Lake Izabal in 1946 and 1947, no *Profundulus* was obtained or expected. The locality

TABLE XI

DORSAL AND PECTORAL FIN-RAY COUNTS IN *PROFUNDULUS LABIALIS*

Figures in parentheses after localities indicate the number of collections.

Locality*	Dorsal Rays								Pectoral Rays							
	11	12	13	14	15	16	No.	Ave.	16	17	18	19	20	21	No.	Ave.
Río Negro Basin																
Ríos Salamá and Rabinal (3).	1	35	46	4	1	..	87	12.64	..	1	20	108	44	1	174	19.14
Río Carchelá (1)	1	2	21	5	1	..	30	13.10	..	..	14	31	15	..	60	19.02
La Primavera (1)	..	10	16	3	..	..	29	12.76	..	..	4	34	20	1	59	19.31
Uspantán and Sacapulas (2) .	..	15	33	11	1	..	60	12.97	1	3	17	62	36	..	119	19.08
Aguacatán to Quiché (3) . . .	2	34	42	12	..	..	90	12.71	..	..	20	99	56	5	180	19.25
NE of Huehuetenango (1). . .	1	3	11	5	..	..	20	13.00	..	1	6	21	12	..	40	19.10
Río Polochic Basin																
Near Tamahú (1).	..	4	18	7	1	..	30	13.17	..	..	7	47	6	..	60	18.98
Finca Pansamalá (1).	..	..	3	7	2	..	12	13.92	..	..	10	12	2	..	24	18.67
Three localities†	..	49	37	5	..	..	91	12.52	1	6	68	100	7	..	182	18.58
Río Chicoy (1)	..	11	10	..	..	..	21	12.48	1	..	8	29	4	..	42	18.83
San Cristóbal (1).	1	21	7	1	..	..	30	12.27	1	7	40	12	..	..	60	18.05
Interior Basin																
Lake Lemoa (1)	..	9	18	3	..	..	30	12.80	..	1	5	45	9	..	60	19.03
Río Motagua Basin																
Near Chichicastenango (1). .	..	1	12	8	8	1	30	13.87	..	1	9	41	8	1	60	18.98
Concuá and Granados (2) . .	1	5	32	2	..	..	40	12.87	..	..	..	27	50	3	80	19.70
Pacific Drainage																
W of Totonicapán (1)	5	16	9	..	..	..	30	12.13	..	2	20	35	3	..	60	18.65
Lake Atitlán and E (4)	..	6	32	34	7	2	81	13.59	2	4	21	98	37	..	162	19.01
Río de Chiapa Basin																
Ríos Saleguá and Canibal (2).	..	13	34	11	2	..	60	13.03	..	2	27	55	29	7	120	19.10
W and E of Aztlán‡ (2) . . .	..	2	23	22	..	..	47	13.43	..	..	..	15	60	18	93	20.03
Chiapa and Paso Chiapa (2) .	9	39	18	1	..	..	67	12.16	..	5	76	43	8	..	132	18.41
Ríos Salado and Chico (2) . .	1	21	23	5	..	..	50	12.64	..	..	1	49	44	6	100	19.55

*All localities are in Guatemala and are of Atlantic drainage except as indicated.
†Finca Chichén, near Patal, and at Purulhá.
‡This and the following localities are in Chiapas, México.

"Yzabal" is therefore regarded as an error. As noted by Carl L. Hubbs on September 10, 1953, the entry for the locality after BM 1.26.1864.390 (the catalogue number for the two specimens in question) is blank and "Yzabal" appears only under number 380 *(Gerres)*, several lines above.

Interior Basin. —Lake Lemoa (Maps 2 and 3), seven and one-half miles by road due south of Santa Cruz Quiché, is a small lake occupying a depression between a branch of the Río Motagua and the main headwater part of that stream just northwest of Chichicastenango. It is roughly oval, comprises approximately 30 acres, and is about 6,700 feet above sea level. Only low ridges surround the basin, the lowest along the southern and western borders. The lake is productive, with thick beds of a broad-leaved *Potamogeton,* as well as *Chara* and fine grass along shore, and a bottom mostly of thick mud. Natives reported that it has never been known to overflow or to go dry, although its level fluctuates greatly; it has neither inlet nor outlet, and obtains its water supply during the rainy season (May to October). Because of the high elevation, evaporation is insufficient during the dry season to desiccate the lake before the onset of the rainy season. Our very brief study of the divides and of available drainage maps (including a fine aerial photograph) suggests that, if a former surface connection existed (as it must have if any of the fishes are native), it was undoubtedly into the basin of the Río Motagua.

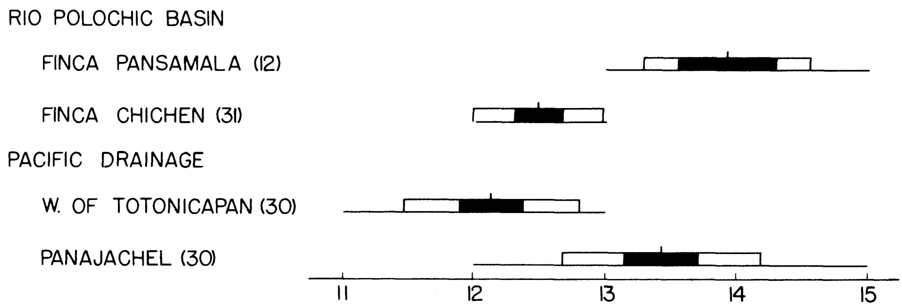
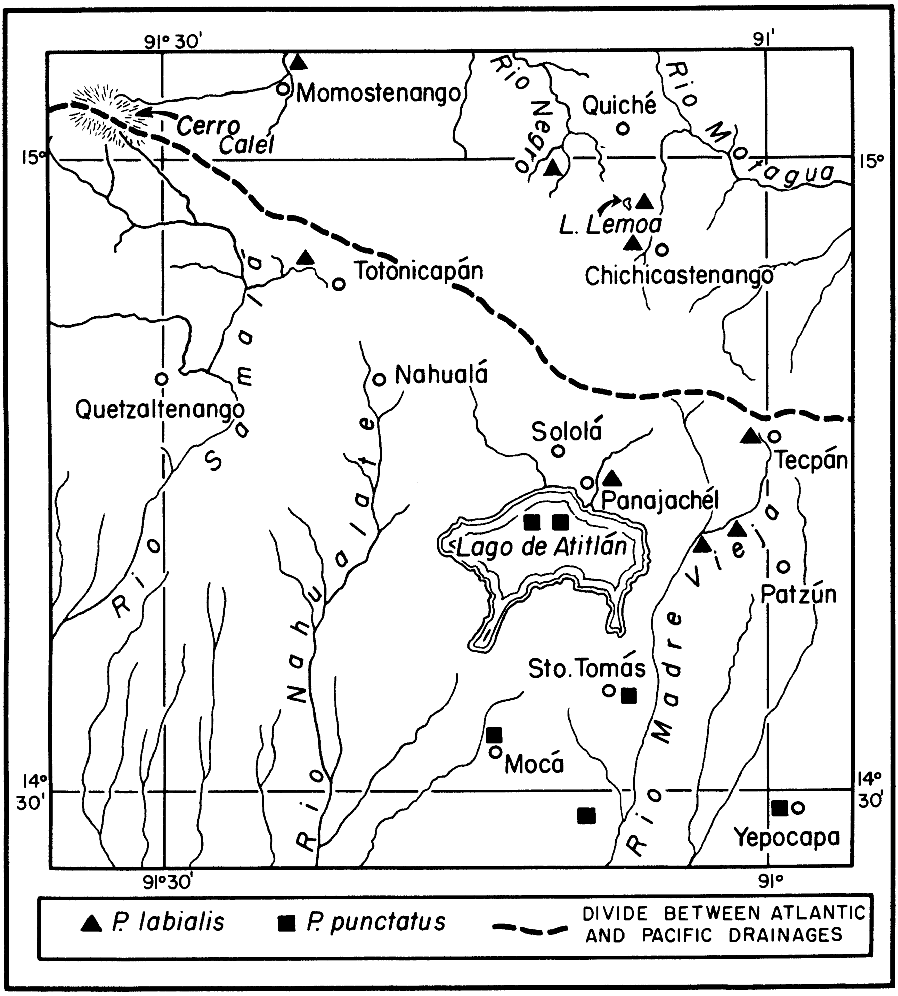


Fig. 5. Number of dorsal fin rays in selected samples of *Profundulus labialis*. For explanation, see Fig. 3.

Three species of fish were found in this lake on April 1, 1947: *Cyprinus carpio, Profundulus labialis,* and *Mollienesia sphenops.* Natives said that the carp had been introduced about 14 years earlier, but that the "pescaditos" had always been in Lake Lemoa. I consider it very doubtful if *Mollienesia* is native. In the Río Motagua drainage I know of no population of *M. sphenops* closer to Lake Lemoa by water than that at Concuá (about 2,300 ft.), 17 air-line miles south-southwest of Rabinal. This species is found in the Highlands, between 4,000 and 5,000 feet, only in the Río de las Vacas (Motagua drainage, Atlantic slope) north of Guatemala City, and in the Río de las Vacas (Michatoya drainage, Pacific slope) south of that city. That a species unfitted for life in swift and turbulent waters would have ascended the steep-gradient gorge of the Motagua River and entered Lake Lemoa does not seem likely.

On the other hand, populations of *Profundulus* occur in both the Río Motagua and Río Negro systems, close to Lake Lemoa. On comparing the Lemoa sample with the Motagua collection, from just north of Chichicastenango, and that from the Negro, six miles west-southwest of Quiché, (see Map 3), the Lemoa stock agrees closely in appearance with the Río Negro sample. Both have a large eye, a large broad head, a broad mouth, and a similar color pattern; the Chichicastenango series shows a much smaller eye, a smaller narrower head, a narrower mouth, and a different color pattern. All meristic characters recorded except the number of scales around the body show closer agreement between the Lemoa and Negro stocks (Tables XI-XIII). This may indicate that: (1) the stock of *Profundulus* in Lake Lemoa was introduced by man from the headwaters of the Negro; (2) the noteworthy difference in body scales supports the view that the Lemoa population is native and has differentiated, in isolation, in this character; or that (3) little significance is to be attached to resemblances and differences in these three stocks in view of the variability of this species. The high frequency of individuals of the Lake Lemoa sample that have regenerated scales somewhat strengthens the view that the fish may not be native to the lake, as there seems to be no obvious reason why a lacustrine population should have lost scales. Also, this regeneration may account, in part, for the lower count of body scales.

Río Motagua Basin. — The Río Motagua (Map 2) rises above Chichicastenango, flows north toward Santa Cruz Quiché, and then swings abruptly



Map 3. A part of western Guatemala to show the local distribution of two species of *Profundulus* and localities mentioned in the text. The two symbols for *P. punctatus* in Lake Atitlán indicate (1) the types of *P. pachycephalus*, collected by Salvin about 1862, and (2) specimens secured by Eisen in 1902. No other collections of this species from the lake are known.

eastward and northeastward for about 230 miles to enter the Bahía de Omoa at the boundary between Guatemala and Honduras.

Only three samples of *Profundulus*, one of which is small, are available from this drainage. Two collections were obtained from the main river — one at the road crossing just west of Chichicastenango and the other at Concuá; the third collection came from a tributary south of Granados, which lies just to the northeast of Concuá.

The samples from the two river collections are similar in coloration, body form, and proportions, but they contrast sharply in average number

TABLE XII

ANAL AND CAUDAL FIN-RAY COUNTS IN *PROFUNDULUS LABIALIS*

Figures in parentheses after localities indicate the number of collections.

Locality*	Anal Rays							Caudal Rays								
	13	14	15	16	17	No.	Ave.	18	19	20	21	22	23	24	No.	Ave.
Río Negro Basin																
Ríos Salamá and Rabinal (3).	..	16	55	16	..	87	15.00	..	..	19	25	42	1	..	87	21.29
Río Carchelá (1)	1	..	16	12	1	30	15.40	..	1	13	13	3	..	..	30	20.60
La Primavera (1)	..	1	25	4	..	30	15.10	..	..	1	12	16	..	..	29	21.52
Uspantán and Sacapulas (2) .	..	6	28	22	4	60	15.40	..	..	16	13	29	2	..	60	21.28
Aguacatán to Quiché (3) . . .	1	15	45	25	4	90	15.18	..	..	12	25	52	1	..	90	21.47
NE of Huehuetenango (1) . .	..	3	12	5	..	20	15.10	..	2	10	4	2	..	..	18	20.33
Río Polochic Basin																
Near Tamahú (1)	..	2	9	16	3	30	15.67	..	..	..	17	12	1	..	30	21.47
Finca Pansamalá (1).	..	..	..	5	7	12	16.58	..	..	4	6	2	..	..	12	20.83
Three localities†	..	24	46	21	..	91	14.97	..	4	27	36	22	2	..	91	20.90
Río Chicoy (1)	..	3	16	2	..	21	14.95	..	..	6	6	9	..	..	21	21.14
San Cristóbal (1).	1	17	10	2	..	30	14.43	..	3	8	11	8	..	..	30	20.80
Interior Basin																
Lake Lemoa (1)	..	2	18	9	1	30	15.30	..	..	5	4	16	3	1	29	21.69
Río Motagua Basin																
Near Chichicastenango (1). .	..	..	10	14	6	30	15.87	..	..	..	1	22	4	3	30	22.30
Concuá and Granados (2) . .	..	1	17	21	1	40	15.55	..	..	9	4	22	3	1	39	21.56
Pacific Drainage																
W of Totonicapán (1).	..	5	14	10	1	30	15.23	..	2	14	9	5	..	..	30	20.57
Lake Atitlán and E (4) . . .	..	4	31	39	6	80	15.59	..	..	16	28	32	..	..	76	21.21
Río de Chiapa Basin																
Ríos Saleguá and Canibal (2).	1	2	25	27	5	60	15.55	..	..	16	12	29	1	2	60	21.35
W and E of Aztlán‡ (2) . . .	..	..	18	28	1	47	15.64	..	..	11	19	16	1	..	47	21.15
Chiapa and Paso Chiapa (2) .	2	12	44	9	..	67	14.89	4	18	31	10	4	..	..	67	19.88
Ríos Salado and Chico (2) . .	..	1	17	23	8	49	15.77	..	..	12	15	22	1	..	50	21.24

*All localities are in Guatemala and are of Atlantic drainage except as indicated.
†Finca Chichén, near Patal, and at Purulhá.
‡This and the following localities are in Chiapas, México.

of dorsal rays (Table XI). Other meristic characters, however, do not show significant differences. The eye is somewhat smaller and the head is definitely shorter in the Concuá race than in the Chichicastenango population. In contrast, the tributary sample has a large eye and conspicuously different coloration: the back and sides, down to the level of the middle of the eye, are dark brown (in alcohol), whereas the area below is a yellowish green, thereby giving a distinctly bicolored appearance to the three adult specimens. The head is notably larger than in the Concuá stock but only somewhat larger than in the Chichicastenango sample. The meristic characters of the tributary stock are generally intermediate between the two river populations except for caudal rays and body scales (Tables XI-XIII). The caudal rays (nine specimens countable) average two fewer than either of the other stocks, and the body scales (16 specimens) average more than one fewer. This is probably due, in part, to the small size of the sample, to the small size of the individuals (as affecting the caudal count; see Miller, 1948: 54-55), and to the difficulty of making accurate body-scale counts on small specimens.

It is obvious that *Profundulus labialis* gained access to the Motagua by way of the Río Negro (see p. 51).

Pacific Drainage. — The natural occurrence of *P. labialis* in Pacific streams, or in waters formerly tributary to the Pacific, may be questioned (see pp. 18-20). It is known to me only from the basin of the Río Samalá just west of Totonicapán, from a tributary to Lake Atitlán, where it was evidently introduced (see p. 20), and from the headwaters of the Río Madre Vieja (three collections), just east of Lake Atitlán (Map 3). All of these are recent collections, made during the period 1935-49.

There is a remarkable similarity in body form and proportions (head length, eye diameter, mouth width, dorsal fin position) between the samples from the Río Samalá, the Río Panajachél (Lake Atitlán), and the lowermost of the Río Madre Vieja collections. The Samalá sample is noticeably darker than the other two (perhaps partly because of longer preservation in formalin) and differs significantly from them in certain counts, especially the number of dorsal rays which averages more than one ray fewer (Table XI; see also Fig. 5). In the two uppermost collections from the Madre Vieja (UMMZ 158446 and ANSP 64747-79), the head is consistently larger and the coloration is dark, as in the Samalá series. The difference in coloration between the lowermost and the upper Madre Vieja samples is probably environmental, for the lower of the two upper samples was taken almost entirely in muddy vegetation, whereas the lowermost sample (USNM 144404), came from a section of the same stream, two and one-half miles below, which lacked vegetation. The lowermost collection and that from Río Panajachél show an even closer resemblance than that observed between the Samalá stock and the other two, for there is agreement here in coloration as well as in details of body form and proportions. The habitat was not described (Fowler, 1936: 520) for the uppermost sample (listed by him under *P. punctatus*) from the Río Madre Vieja.

The status of these forms is not entirely clear, but if *P. labialis* was introduced into Lake Atitlán (as seems assured) it is reasonable to assume that it was also stocked in the upper Río Madre Vieja, which is crossed and followed by the main highway from Lake Atitlán to Guatemala City. The presence of this species in the Río Samalá may have been brought about by stream capture of an upper tributary of Río Momostenango by a branch of Río Samalá in the region of Cerro Calel; study of aerial photographs of this region indicates that this is the only plausible area where a transfer could have occurred (Map 3). Dr. Stuart advises me that there are high, impassable falls in the Samalá below Quetzaltenango, which may explain why *P. punctatus* apparently has not penetrated the upper part of this river. Unfortunately, no samples of *Profundulus* have been taken from the upper Río Nahualate (near Nahualá), the stream to the east of Lake Atitlán between the lake and Río Samalá. No fish were seen in this stream during a brief stop at Nahualá on May 11, 1946.

Río de Chiapa Basin. — The Río de Chiapa (item 6, Map 1) rises in the western highlands of Guatemala, just west and south of Huehuetenango (Map 2), flows northwestward for about 200 miles through the highlands of Chiapas, and then turns northward for about 120 more miles where it joins the Río Usumacinta to enter the Gulf of México (Gulf of Campeche) about 15 miles farther north. In the highlands of México its chief tributaries enter from the south. The river is generally known as the Río Grijalva, or Río de Chiapa, but it is locally called the Río Grande in its upper part.

Twenty-three collections, mostly small, are available from this drainage. Elevations at these stations vary from about 1,400 at Chiapa de Corzo,

TABLE XIII

SCALE COUNTS IN *PROFUNDULUS LABIALIS*

Figures in parentheses after localities indicate the number of collections.

Locality*	Lateral Scales							Scales Around Body								
	35	36	37	38	39	No.	Ave.	30	31	32	33	34	35	36	No.	Ave.
Río Negro Basin																
Ríos Salamá and Rabinal (3).	..	15	57	14	1	87	37.01	2	5	33	19	22	..	1	82	32.71
Río Carchelá (1)	..	4	20	6	..	30	37.07	..	..	12	4	13	..	..	29	33.03
La Primavera (1)	..	1	20	8	..	29	37.24	2	4	20	2	..	..	..	28	31.79
Uspantán and Sacapulas (2) .	..	..	25	34	1	60	37.60	..	..	4	23	28	1	4	60	33.63
Aguacatán to Quiché (3) . . .	..	5	45	37	2	89	37.40	..	..	14	12	39	9	8	82	33.82
NE of Huehuetenango (1). . .	2	14	3	1	..	20	37.15	1	1	15	1	2	..	..	20	32.10
Río Polochic Basin																
Near Tamahú (1)	..	..	7	21	2	30	37.83	..	..	..	4	22	3	..	29	33.97
Finca Pansamalá (1).	..	7	5	..	..	12	36.42	2	1	5	2	..	..	..	10	31.70
Three localities†	2	35	46	7	1	91	36.67	1	..	10	2	14	..	3	30	33.33
Río Chicoy (1)	..	..	13	8	..	21	37.38	..	3	14	..	3	1	..	21	32.29
San Cristóbal (1).	1	13	15	1	..	30	36.53	5	2	9	4	5	..	..	25	32.08
Interior Basin																
Lake Lemoa (1)	..	1	24	5	..	30	37.13	..	..	18	2	2	..	..	22	32.27
Río Motagua Basin																
Near Chichicastenango (1) .	..	5	20	5	..	30	37.00	..	..	1	3	19	3	..	26	33.92
Concuá and Granados (2) . .	..	2	22	11	..	35	37.26	..	..	5	6	17	1	..	29	33.48
Pacific Drainage																
W of Totonicapán (1).	..	2	17	11	..	30	37.30	..	1	7	7	15	..	..	30	33.20
Lake Atitlán and E (3) . . .	..	11	47	2	..	60	36.85	1	9	19	16	8	..	..	53	32.40
Río de Chiapa Basin																
Ríos Saleguá and Canibal (2).	..	2	28	27	3	60	37.52	..	1	7	11	27	5	8	59	33.88
W and E of Aztlán‡ (2) . . .	..	..	16	30	1	47	37.68	4	5	26	8	4	..	..	47	32.06
Chiapa and Paso Chiapa (2) .	2	27	25	3	..	57	36.51	5	6	2	2	2	..	..	17	31.41
Ríos Salado and Chico (2) . .	..	15	29	6	..	50	36.82	7	3	10	7	14	1	2	44	32.66

*All localities are in Guatemala and are of Atlantic drainage except as indicated.
†Finca Chichén, near Patal, and at Purulhá.
‡This and the following localities are in Chiapas, México.

Chiapas, to 6,000 feet on the Río Saleguá, Guatemala. Only two of the samples are from Guatemala; the remainder are from the highlands of Chiapas. Eight of the collections (including the two from Guatemala) contain series of workable size and these have been studied in detail. At least four variously distinct types of *Profundulus labialis* are represented in the material at hand, but the characters of most of these intergrade with those of adjacent as well as distant populations.

Five samples were selected to show extremes of variability in the number of scales, vertebrae, and caudal rays (Figs. 3-4, 6; see also Tables XI-XIII). The sample from Río Saleguá, Guatemala, represents a relatively slender, short-headed race, with a moderate-sized eye and relatively narrow mouth. The head length stepped into the standard length yielded ratios of 3.6 to 3.8 in 20 specimens from this collection and one from nearby Río Canibal. On the contrary, the sample from a stream west of Aztlán revealed a race with a long, broad head, a large eye, and a broad mouth. Head length to standard length ratios of 3.1 to 3.4 resulted in seven specimens of a size similar to those of the two Guatemalan populations above. The dorsal fin is also more posterior, giving ratios of 1.9 to 2.2, rather than 1.7 to 1.95, in 20 specimens from Aztlán and 20 from the combined Guatemalan stations. (The ratios represent the distance between caudal base and dorsal origin projected forward to snout tip). In addition to these marked differences between the Aztlán collection and the two headwater populations, the pectoral rays average greater (Table XI), the body-circumference scales are fewer (Table XIII), and there are notably fewer vertebrae in the Aztlán stock than in the Canibal sample (Fig. 4). The Saleguá series has almost precisely the same number of vertebrae, however, as the sample from west of Aztlán. Moreover, the collection from just east of Aztlán (the western, sluggish stream is tributary to the swift, eastern one) is somewhat intermediate between the western sample and the headward, Guatemalan races.

The sample from a spring near Chiapa de Corzo is poorly preserved, but appears to resemble the Río Saleguá race closely. Ratios for the dorsal position in these specimens (38 to 65 mm.) vary from 1.7 to 2.0, dominantly from 1.8 to 1.9 (only one specimen at each extreme); the dorsal is thus slightly farther back than in the Guatemalan races. Again the differences between this sample and adjacent ones are striking; the pale coloration is presumably due largely to improper preservation. In counts this race has the smallest average number of dorsal and anal rays and scales around the body of any of the samples counted in the Chiapa basin, and is in the lower range for pectoral rays (Tables XI-XIII).

A large series from the Río de las Flores at Paso Chiapa (Map 1), in the drainage of the Río de la Venta, differs from all other populations in the Chiapa basin in the long, slender body and the generally more pronounced spotting on the sides, especially below the disrupted lateral band. The collection was made near the end of the dry season when the river was broken up into a number of wide, shallow (1-2 feet), sandy, interconnected channels. Excessive regeneration of the scales indicates that the individuals secured were badly buffeted during the previous flood stages of the stream, and this has rendered some scale counts so dubious that they have not been used. I strongly suspect that the unfavorable habitat has influenced the condition of the fish so that they have become emaciated, with thin bodies, large eyes, and a peculiarly depressed snout. What effect the regenerated scales may have had on the color pattern is problematical. In some of the smaller specimens (25 to 35 mm.) I note that the eye is relatively smaller and the snout nearly normal, suggesting that if environmental factors have acted to produce or influence the rather extreme characters of this sample, they apparently have not exerted an equal influence on the yearling fish. The collection is extreme also in certain meristic characters (Tables XI-XIII; Chiapa and Paso Chiapa): caudal rays average significantly fewer (Fig. 6), dorsal and pectoral ray counts are low, and the lateral scales and vertebrae (Figs. 3-4) average fewer than in any other collection from the Chiapa basin. The body scales (not recorded here) seem to average fewer than 30 but the accuracy of this enumeration is too questionable to permit acceptance, especially since this count for seven specimens from two additional localities in the same drainage indicates an average of more than 32 scales. The scanty material (9 specimens) at these other stations (between Cintalapa and Palo Grande and at Ortiz Rubio; see Material Examined) does tend to show that most of the extreme characters of the Paso Chiapa series are local, although the depressed snout and the reduced number of scales in the lateral series appear to be retained in these samples as well. Until further collecting is done in the Río de la Venta, I prefer to regard the status of this population as open to question.

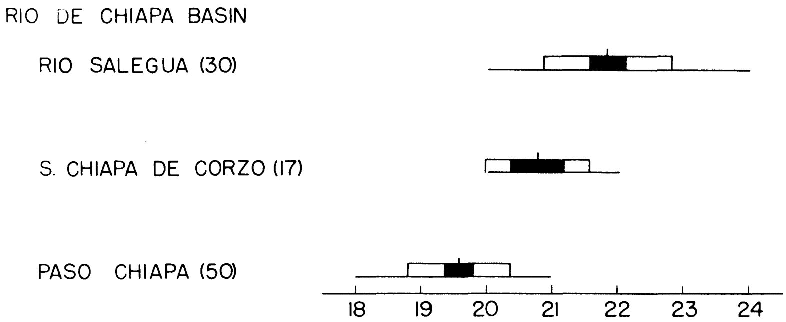


Fig. 6. Number of caudal fin rays in selected samples of *Profundulus labialis*. For explanation, see Fig. 3.

In the Chiapa system, as in all other drainage basins represented by adequate collections, *P. labialis* exhibits striking variations between adjacent as well as distant samples. As in other basins too, at least one sample (from Río Saleguá) is strikingly similar to that in a different (Pacific) drainage (Río Samalá). The erratic nature of these variations cautions me against nomenclatorial recognition of populations in this basin and all are referred to *Profundulus labialis*.

Status of *Tlaloc mexicanus*. — Reasons for regarding this nominal genus as a synonym of *Profundulus* have already been presented (p. 9). The placement of the species is considered here. It was described by Alvarez and Carranza (1951) on the basis of 13 small specimens from Ocosingo (Map 1), the type locality, 36 airline miles northeast of Cuidad de Las Casas, Chiapas, México, and one specimen (the largest; see their Fig. 1) from El Real, 23 airline miles east-northeast of Ocosingo in the same state. These localities lie in the basin of the Río Jataté (item 7, Map 1), a tributary of the Río Usumacinta by way of the Río Lacantún, and are about 2,650 and 2,100 feet, respectively, above sea level. The lower part of the Jataté flows through tropical Atlantic lowlands, where no specimens of *Profundulus* have been taken, and hence the populations in the upper Jataté are probably effectively isolated by ecological barriers from other populations in the upper Usumacinta (Río Negro) drainage.

In considering the status of the Jataté *Profundulus*, three specimens (2 paratypes of *Tlaloc mexicanus*, UMMZ 162154, and one male from El Real, UMMZ 161767) are available for study. These seem clearly referable to *P. labialis*. The meristic data follow: dorsal 11, 12, 13; anal 15, 16, 17; pectorals 18-18, 20-19; caudal 18 (?), 20, 21; lateral scales 34 (35 on right side), 35, 36; scales around peduncle 20 in all; scales around body perhaps 30 to 32 (all counts questionable); scales between midline of back and lateral series apparently 5 (regenerated scales and the small size of one paratype make the figure tentative); gillrakers 15, 16; and vertebrae 35, 35, 36. In the naked preorbital, in details of squamation on the caudal fin, in adult coloration, dorsal origin, shape of anal fin in the female, shape of lower jaw, rostral pores on the snout of the adult, and the width of the preorbital (Table II), the specimens agree well with *labialis*. The eye is rather large.

The scale and vertebral counts, however, place these specimens at the extreme low range for *P. labialis* (see Table XIV, which includes the above data).

The counts given by Alvarez and Carranza (1951) are, in general, lower than mine and mostly reflect differences in methods of counting. Some errors are evident, however, for they recorded only 16, rarely 15 or 17, principal caudal rays, which is below the known variation for *Profundulus* (Table XIV). I count 20 in one paratype, possibly 18 in the other, and 21 in the El Real specimen. The error could be due, in part, to the small size of their specimens, for the caudal rays become fully differentiated at a later stage than do the rays of the other fins (Miller, 1948: 54-55). Their figure of the paratype from El Real (37.2 mm.) very closely resembles the single Michigan specimen (49 mm.) from the same place, except that the lateral band as drawn is too prominent and the dorsal fin is too far back.

It may well be that further collections from the Río Jataté drainage will reveal populations of *P. labialis* characterized by a reduced number of scales and vertebrae and that an endemic subspecies in this isolated system will be recognizable. In that event, the subspecific name *mexicanus* is available.

Range. — *Profundulus labialis* is nearly restricted to the Atlantic drainage from central Guatemala to central Chiapas, México, occurring in the headwaters of the Río Motagua, Río Negro (of the Usumacinta system), Río Polochic, Río de Chiapa (or Grijalva), and the Río Jataté (Map 1). It is known from Pacific tributaries only in the highlands of Guatemala (Map 3): Río Samalá, west of Totonicapán, the Río Panajachél, tributary to Lake Atitlán (where introduced), and the Río Madre Vieja, just east of Lake Atitlán (where possibly planted). Its altitudinal range is from about 1,400 feet in the Chiapa drainage to 8,000 feet near Totonicapán.

Profundulus candalarius Hubbs

Pl. IX

Profundulus candalarius Hubbs, 1924: 15-16 (orig. descr. based on 2 spec.; type loc.: spring at Candalaria, Guatemala).

Nothing has been published on this species since the original description appeared, and evidently no new material was collected between 1906 and 1941. Through the kind efforts of Salvador Coronado, who in 1941 was encouraged to collect by Norman E. Hartweg, there are now 273 yearlings to adults available from the Río Grande de Comitán in south-central Chiapas, México. Unfortunately, however, most of this material is not well preserved, and none of the specimens is as large as either of the types. The holotype and allotype (CNHM 9071 and 9072, respectively) have also been studied.

The characters which distinguish *P. candalarius* from *P. labialis* are associated with a general reduction in number of segmental parts (Table XIV), an approach to the *punctatus* group in length of anal fin and squamation of preorbital, and a consistently wider separation between the mandibular and the preopercular canals. As pointed out by Hubbs (1924: 16), the dorsal fin is more posterior than in *P. punctatus* (including *oaxacae*), but this fin is just as far back in some collections of *P. labialis*, as from just west of Aztlán in the nearby Río de Chiapa basin (p. 41). It is, however, consistently more posterior in *candalarius* than in the majority of the races of *labialis*: the distance between caudal base and dorsal origin when projected forward with dividers gave ratios, in 46 specimens (27-60 mm. S.L.), of 1.9 (4), 1.95 (4), 2.0 (17), 2.1 (16), 2.15 (2), and 2.2 (3); the value was approximately 2.15 for the holotype (72 mm.) and 2.2 for the allotype (68.5 mm.). The larger scales provide the easiest means for separation from *labialis* (see Key, p. 16), but other differences are believed to be more significant. The preorbital is consistently better scaled: in 50 specimens studied, 44 have a single, embedded scale (usually rather small) on each side whereas only one is naked on both sides and the remainder have at least 1 or 2 scales on one or both sides. The holotype and allotype have a single scale on each side. The mandibular and preopercular canals are typically more widely separated: in 50 specimens examined the canals were united on both sides in only 1, almost united (joined by an open groove) in 15, rather narrowly separated in 29 (including the types), and well separated in 3. The anal fin is not greatly elongated, as it typically is in the larger adults of *labialis*, and in this feature *candalarius* approaches the *punctatus* group. The color pattern on the sides, the absence of a humeral spot, the configuration of the head, mouth, and jaws, the position of the dorsal fin, and the wide preorbital all stamp this species as a member of the *labialis* group (Pls. VII-IX).

Type locality. —According to the original label with the holotype, the type specimens came from a limestone spring at Candalaria, 6 leagues from Nentón, Guatemala, near the Mexican boundary. They were collected by O. F. Cook on June 1, 1906. After considerable search, with assistance from L. C. Stuart, I was able to approximate the location of Candalaria; it lies some 11 airline miles NNW of Nentón almost on the border between Guatemala and México (Map 2). By trail from Nentón, the distance would reasonably amount to "6 leagues" (about 18 miles). Candalaria is evidently on or near the edge of a limestone plateau which extends northward toward the basin of the Río Grande de Comitán; the elevation is about 1,000 meters (3,300 feet; see Claudio Urrutia map of Guatemala, 1923). The assertion, evidently by the collector, that the spring lies in the basin of the Río de Chiapa, is open to question since the species appears to be otherwise confined to the Comitán basin and is absent from the 23 samples of *Profundulus* taken in the Chiapa drainage. Hydrographic relationships in limestone country are sometimes difficult to determine accurately, and it may be assumed on zoogeographic grounds that the spring at Candalaria is (or was) connected in some way with the basin of the Río Grande de Comitán.

Variation. — In addition to the two type specimens, five collections are available from the basin of the Río Grande de Comitán. This stream rises just to the north of Comitán (elevation about 5,200 feet) and flows in a southeasterly direction for about 26 miles to terminate in Lake Tepancuapán about 5,000 feet), near the border of Guatemala (Map 1). Below this point the drainage of the stream is obscure, for its waters disappear into a cave, but it is believed to have a subterranean connection with the Río Santo Domingo, a tributary of the Río Jataté of the Usumacinta basin. Fish populations in the Río

Grande de Comitán are thus effectively isolated from those of surrounding basins, and this has been a major factor in the evolution of the remnant fish fauna. Only three other species occur in collections from this basin: a characin, a poeciliid, and a cichlid.

The five collections from the Comitán were taken in the dry season, April 17 to 19, 1941, and are listed at the end of this paper (see Material Examined). A collection from Lake Montebello (just E of Lake Tepancuapán) contained no *Profundulus*. Except for some skewness in number of dorsal rays, the meristic data for these populations (that from San José del Arco not counted) show normal frequency distributions (Table XIV). The preponderance of 11 dorsal rays results from the fact that all populations counted except one have 11 or 12 dorsal rays, whereas that from the Comitán (1.5 km. E of Comitán) has a strong mode at 11. This is not considered to be of systematic significance since the population only 0.5 km. distant (from La Ciénega) has 11 or 12 dorsal rays.

Comparison of the five collections reveals that they are more variable in external morphology than in meristic characters. The sample from Yocnajab is extreme in having an elongated, cone-shaped head which is notably depressed in the snout region, a large eye, a broad mouth, and a broad, strong lower jaw which is rather abruptly oblique. In these respects this sample agrees well with the types. In the population from La Ciénega, the head is shorter, its dorsal profile evenly concave (rather than convex), the eye is smaller, the mouth is narrower, and the lower jaw is not so broad and not abruptly oblique. The sample from the Comitán just 0.5 km. from La Ciénega is somewhat intermediate in these characters between the Yocnajab and Ciénega populations, but approaches the Ciénega type more closely. The collection from Santo Tomás (also on the river) seems to be like the uppermost Comitán race, just discussed, but is so poorly preserved that an accurate comparison is not possible. The sample from San José del Arco (just below Santo Tomás) closely approaches the extreme type at Yocnajab, but is not quite so modified.

Thus, within the short drainage of the Comitán, extremes of body form and shape occur, along with intermediate types, thereby suggesting environmental modification of proportional characters. The extreme type occurs in the main river where, above and below, less modified races also exist. The type specimens from Candalaria, less than 20 airline miles distant in Guatemala, closely resemble the extreme form in the Río Grande de Comitán; the considerably larger size of the types, however, makes a critical comparison of body proportions difficult.

Range. — Known only from the Río Grande de Comitán, a stream of interior surface drainage, in south-central Chiapas, México, and from a limestone spring at Candalaria, Guatemala, which presumably is (or was) connected in some way with the Comitán basin.

Profundulus hildebrandi Miller

Pls. V – VI

Profundulus hildebrandi Miller, 1950: 22-30, Pl. 1 (orig. descr., based on 516 specimens; type loc.: Laguna María Eugénia at San Cristóbal de Las Casas, Chiapas, México; elev. 7,260 feet).

TABLE XIV

NUMBER OF FIN RAYS, SCALES, GILLRAKERS, AND VERTEBRAE IN THE SPECIES OF *PROFUNDULUS**

Species	Dorsal Rays							No.	Ave.
	10	11	12	13	14	15	16		
punctatus	13	140	243	125	23	1	..	545	12.01
guatemalensis .	16	216	472	237	74	10	..	1025	12.16
labialis	..	22	298	452	146	23	3	944	12.85
candalarius . . .	3	54	34	2	..	..	..	93	11.38
hildebrandi . . .	..	16	35	19	..	..	..	70	12.04

Species	Anal Rays								No.	Ave.
	11	12	13	14	15	16	17	18		
punctatus	1	20	164	231	103	24	4	..	547	13.92
guatemalensis .	..	21	238	505	231	31	2	..	1028	14.02
labialis	..	..	6	116	459	314	48	1	944	15.30
candalarius . . .	..	1	25	55	11	1	..	..	93	13.85
hildebrandi . . .	..	..	..	6	34	28	2	..	70	15.37

Species	Pectoral Rays								No.	Ave.
	15	16	17	18	19	20	21	22		
punctatus	..	12	191	528	257	27	..	..	1015	18.09
guatemalensis .	..	9	188	753	835	147	5	..	1937	18.48
labialis	..	6	33	380	974	450	42	1	1886	19.04
candalarius . . .	..	10	76	91	6	..	..	..	183	17.51
hildebrandi . . .	1	2	35	79	6	..	..	..	123	17.71

Species	Caudal Rays									No.	Ave.
	17	18	19	20	21	22	23	24	25		
punctatus	..	7	66	137	158	83	28	7	..	486	20.73
guatemalensis .	..	13	45	193	320	243	97	22	6	939	21.22
labialis	..	4	30	232	273	369	20	7	..	935	21.13
candalarius . . .	2	26	34	28	2	..	..	..	..	92	19.02
hildebrandi . . .	..	2	5	37	13	..	..	..	..	57	20.07

Species	Lateral Scales									No.	Ave.
	31	32	33	34	35	36	37	38	39		
punctatus	55	191	188	53	1	..	..	..	..	488	32.49
guatemalensis .	11	248	474	219	16	1	..	..	..	969	32.98
labialis	..	..	..	1	6	164	515	211	12	909	37.06
candalarius . . .	..	..	8	72	4	1	..	..	..	85	33.98
hildebrandi . . .	..	..	..	4	41	22	1	..	..	68	35.29

TABLE XIV (Cont.)

Species	Scales Around Body													No.	Ave.
	24	25	26	27	28	29	30	31	32	33	34	35	36		
punctatus	2	3	220	25	128	10	33	..	..	..	..	..	..	421	27.03
guatemalensis .	..	..	139	47	503	21	41	2	..	..	..	..	..	753	27.71
labialis	..	..	..	..	..	..	24	39	214	129	237	24	23	690	32.99
candalarius . . .	..	..	..	1	23	6	32	..	1	..	..	..	..	63	29.16
hildebrandi . . .	..	..	..	1	18	10	31	6	1	..	..	..	..	67	29.39

Species	Gillrakers										No.	Ave.
	14	15	16	17	18	19	20	21	22	23		
punctatus	1	2	8	19	20	13	7	4	4	2	80	18.25
guatemalensis .	1	10	17	40	45	17	3	..	..	..	133	17.36
labialis	..	1	5	23	54	46	9	6	..	..	144	18.32
candalarius . . .	..	1	10	23	11	6	..	..	..	..	51	17.21
hildebrandi . . .	2	5	22	18	3	..	..	..	..	..	50	16.30

Species	Vertebrae									No.	Ave.
	31	32	33	34	35	36	37	38	39		
punctatus	11	89	119	42	..	..	..	..	..	261	32.73
guatemalensis .	3	57	153	89	10	1	..	..	..	313	33.16
labialis	..	..	..	..	7	62	144	36	3	252	36.87
candalarius . . .	..	..	8	29	4	..	..	..	..	41	33.90
hildebrandi . . .	..	..	..	..	16	20	1	..	..	37	35.59

*Including all available type specimens and a number of small collections not included in Tables IV-IX, XI-XIII.

Since no new material has been received, there is little that I wish to add to the original description of this distinctive species. *P. hildebrandi* agrees in most technical characters with the *labialis* species group for it has a wide, naked preorbital (or there may be a single, embedded scale); only about a third of the base of the caudal fin is densely scaled; the coloration is light, with horizontal rows of light spots and with no dark lateral band or humeral spot; the rostral pit organs (Fig. 2A) are developed as open pores in the adult; the origin of the dorsal fin is behind that of the anal; and the anal fin of the adult female is notably elongated. In the broad, heavy, projecting lower jaw and the long and broad head, *P. hildebrandi* closely resembles *P. guatemalensis*, of the *punctatus* species group. The number of scales and vertebrae is intermediate between the two species groups (if *candalarius* is excluded) and the number of gillrakers averages fewer than in any of the other species (Table XIV). Its specific attributes are a uniformly slender body with a large, broad head, a broad mouth, a strongly-projecting lower jaw, and the diagnostic coloration: the narrow, irregular vertical bars (Pl. VI) of the young and juveniles are mostly continuous (or nearly so) below the mid-sides and thus are more conspicuous than in the other species, in which they fade out in this region; the general pigmentation is coarser and more profuse and extends downward on the sides of the head and body and, in adults, to the ventral surface, whereas in the other species the chromatophores are generally smaller, less profuse, scarcely extend below the level of the lower rim of the orbit, and the ventral surface is essentially unpigmented; the predorsal streak, on the midline of the back, is narrower and fades out before reaching the occiput; there is a dark spot or blotch at the base of the caudal fin of the adults which is usually rather faint but discernible, although uncommonly obsolete (in 30 adults only 2 had no trace of the spot; it is never developed in the other species).

The lateral-line system of pores on the head region (Fig. 2; Pl. V) is consistently better developed in *hildebrandi*, for the pores are unusually conspicuous and they vary little in position or development. The mandibular and preopercular canals are more frequently united in this species than in others of the genus: in 41 young to adult, the connection is complete, and in 9 additional young the two canals are almost united.

Type locality. — According to information received from Dr. José Alvarez (letter dated March 27, 1951), who visited Laguna María Eugénia in 1951, the type locality has "disappeared," but some other ponds nearby are populated with the same species. Dr. Alvarez also wrote that the waters of this limestone region do not drain to the Río de Chiapa by way of a precipitous gorge, as previously reported (Miller, 1950: 27), but discharge by way of a subterranean river supposedly into the Chiapa basin — although this is without confirmation.

Data on the habitat, when visited on April 14, 1941, by Norman Hartweg and Salvador Coronado, were misplaced at the time this species was described. The laguna, which lay near the southeastern edge of Las Casas, was 1 to 2 feet deep with clear water and dense vegetation along shore (none in the outlet). The pond bottom was muddy but at the outlet it was rocky; there was little current from the overflow of the pond. The shore was described as swampy. The 486 excellently preserved specimens were obtained through the use of rotenone and were fixed in 10 per cent formalin.

Range. — Known only from the high, isolated limestone plateau near San Cristóbal de Las Casas (Map 1) in central Chiapas, México. This town, usually called Ciudad Las Casas (or simply Las Casas), is about 32 miles by airline east of Tuxtla Gutiérrez, the capital of Chiapas, and lies about 7,500 feet above sea level.

DISTRIBUTION AND ORIGIN

The geographical distribution of the five species of *Profundulus* (Map 1) presents problems of interest to the zoogeographer and to the student of geomorphology. Although the Cyprinodontidae as a group are tolerant of wide variations in salinity, *Profundulus* appears to be strictly confined to fresh water and hence is largely or wholly independent of marine dispersal. Whether it has always been so independent is problematical. There are reasons for believing that the two species groups originated in distinct areas of Middle America and that they were subsequently brought together through natural topographic changes, such as stream captures.

The *labialis* group (including *labialis, candalarius* and *hildebrandi*) probably arose in the highlands of Chiapas, México, where all three species now live in isolation. *P. hildebrandi* is confined to a high limestone plateau, not now accessible to other fishes; *P. candalarius* occurs in a nearby but disjunct stream system; and *P. labialis* is generally distributed (along with *P. punctatus*) in those areas of Chiapas not inhabited by either *hildebrandi* or *candalarius*, and in nearby parts of Guatemala.

The restricted habitat and strongly isolated position of *P. hildebrandi* and the fact that it shares fundamental characters with *P. labialis* bespeak an early origin from a common ancestral stock. Its sharply distinctive specific characters further support the view that *hildebrandi* represents an early stage in the evolution of the *labialis* type. The similarity in jaw and mouth configuration between *hildebrandi* and the species of the *punctatus* group is interpreted as the result of secondary convergence rather than as an indication of intimate relationship. This presumed convergence has led to similar feeding habits, for *hildebrandi* appears to be the only species of the *labialis* group which eats mollusks — a common item in the diet of *P. punctatus* and *P. guatemalensis* (as revealed by X-ray photographs). The suggestion is offered that the differentiation of *P. hildebrandi* dates back at least to Pliocene times; the limestone plateau (Mesa Central) on which it lives is dominantly of Cretaceous age and forms the highest mountain mass of Chiapas (Schuchert, 1935: 328; Sapper, 1937, Pl. Vb).

P. candalarius obviously is a relatively recent offshoot from *labialis* that differentiated when the drainage it now inhabits became disrupted from waters populated by the *labialis* stock. In contrast to *hildebrandi*, the characters of *candalarius* indicate that this species is an allopatric representative of *labialis* that has diverged from the parent type due to geographical isolation, which may have taken place at some time during the Pleistocene. On zoogeographic grounds, I postulate that the ancestral stock gained access to the Río Grande de Comitán by way of the Chiapa, rather than the Usumacinta, drainage. Entrance from the Chiapa basin is almost demanded because *P. labialis* is a highland form that is not known to occur below 2,000 feet in the Usumacinta basin. In addition, there is a *Poeciliopsis* in the Comitán which is close to a species of the same genus in the upper Chiapa system. Except for *P. pleurospilus* (usually called *Poecilistes lutzi*), which occurs on both sides of the Isthmus of Tehuantepec, the known species of *Poeciliopsis* are restricted to the Pacific drainage.[10] Hence it is clear that the form in the Comitán was derived from a stock in the Chiapa system, thereby indicating a former connection between the two drainages. Just where this postulated connection took place is problematical.

The distributional pattern of *P. labialis* provides evidence to indicate that this species originated in what is now the basin of the Río Grande de Chiapa rather than, for example, in the adjacent, independent basin of the Río Negro, Guatemala. To support this view, the distribution of the isolated populations on the fringe of the range of this species is considered first.

It is evident that *P. labialis* gained access to the independent drainage of the Río Polochic through a former connection between that system and the

[10]*Poeciliopsis latidens* (Garman), described from "Chihuahua, México," occurs only in streams of northwestern México that drain into the Pacific (Hubbs and Miller, 1954).

Río Negro. Sapper (1901: 91; 1937: 74) stated that at one time the Río Negro flowed eastward into the Polochic instead of making the abrupt horseshoe turn northwest of Salamá which the river now follows (Map 2). The distribution of *Profundulus* in the Polochic basin supports the physiographic evidence, for the genus occurs in that drainage only above 4,000 feet and the only acceptable explanation for its presence in this headwater area is by a former waterway between the two drainages.

The occurrence of *P. labialis* in the upper part of the Río Motagua (unknown below 2,300 feet) is also to be explained by a previous hydrographic connection between this headwater area and that of the Río Negro (Sapper, 1937). It seems plausible to hypothesize that the northward flowing upper part of the Motagua (near Chichicastenango) was formerly a part of the Negro system and was subsequently captured by headward erosion of the Río Motagua (Maps 2-3). That *P. labialis* gained access to the Motagua basin by any other means save a headwater transfer is rendered untenable because of the restricted distribution of the genus in that system.

It is apparent that *P. labialis* did not originate in any river of the Pacific slope, for this species is virtually confined to the Atlantic drainage and its natural occurrence in some waters of the Pacific versant (e.g., Lake Atitlán, formerly a Pacific tributary) is open to question (see pp. 19-20).

The final problem in the distribution of *P. labialis* is now left — namely, did this species enter the Río Negro from the Río de Chiapa or vice-versa? The divide between these two major drainages, in the vicinity of Huehuetenango, is a low, nearly flat plain. The present drainage patterns of the two rivers overlap in this area so that upper tributaries of the Río de Chiapa lie north and east of headward branches of the Río Negro (Map 2). A study of the Claudio Urrutia map (1923), which shows topography as well as river systems, and a consideration of the conclusions reached by Sapper (1901, 1937) on the evolution of the Río Negro, indicate that the Negro beheaded an upper segment of the Chiapa. Indirect evidence also supports the view that the *Profundulus* of the Río Negro was derived from that of the Río de Chiapa. The occurrence of *P. hildebrandi* on a high, isolated plateau that drains toward the Río de Chiapa (Map 1), and the interpretation of this species as an early (Pliocene?) derivative from an ancestral stock common to both *labialis* and *hildebrandi,* reinforces the idea that *labialis* originated in the highlands of Chiapas and spread eastward from that area.

The *punctatus* species group (which includes *punctatus* and *guatemalensis*) probably arose in the highlands of Guatemala, where *P. guatemalensis* is now abundant and is, in many places, the only native fish. *P. punctatus* is regarded as a derivative of *guatemalensis* that has invaded the Pacific lowlands of Guatemala and has spread from there westward nearly to Acapulco and across the Isthmus of Tehuantepec into the Río de Chiapa basin; it also occurs locally in the upper part of the Río Coatzacoalcos, Oaxaca, an Atlantic tributary (Map 1). *P. punctatus* is found at much lower elevations than the parent form, and the two species are not known to occur together. Although *punctatus* has the greatest range of any species of *Profundulus,* it appears to be much less abundant than either *labialis* or *guatemalensis,* presumably because of competition pressure in the comparatively rich faunal areas which comprise most of its known range. At higher elevations (as in Guatemala and in southern

México), where fewer species live, it is notably more abundant and of less restricted habitat than it is in the lowlands.

P. guatemalensis is almost entirely confined to the highlands of Guatemala, but ranges into El Salvador and is known from one collection in the Río Lempa basin of western Honduras. It occurs mostly in streams of the Pacific slope, but has gained access to the basins of the Río Motagua and the Río Negro, of the Atlantic drainage, in Guatemala.

The divide between the Motagua (Atlantic) and Michatoya (Pacific) drainages at Guatemala City (Map 2) is low and flat, and at one time there was a marshy swamp along the southern margin of the city. Rejuvenation of the erosion cycle has resulted in the carving of numerous barrancas which vary from 150 to 500 feet deep (Niederheitmann and León, 1945). The fish fauna of the upper Motagua basin and that of the highland portion of the Michatoya provide zoogeographic evidence for a former waterway across the drainage divide, for several species are common to the two basins. *P. guatemalensis* occurs in the Motagua drainage only in its upper portion, and the species obviously entered that system from the Michatoya or an adjacent stream.

It is perhaps nearly as plausible to assume that the cross-over between the Atlantic and Pacific drainages took place near Chimaltenango (Map 2), to the west of Guatemala City, where the divide is also low and flat and composed of Quaternary deposits (Sapper, 1937; Pl. VI); or that both regions served as migration paths for aquatic organisms.

Profundulus guatemalensis also occurs in the Río Negro (Usumacinta) system, where it has been taken near Rabinal, at San Jerónimo, and in the Río Carchelá (see Map 2 and Material Examined). It has already been hypothesized that *P. labialis* gained access to the Río Motagua through stream capture of a headwater branch of the Negro by that of the Motagua. Such a capture cannot explain the presence of *P. guatemalensis* in the Negro; in fact, the capture must have been in the reverse direction (the Negro cutting off a branch of the Motagua). There is no other plausible region for crossover between the Motagua and Negro systems; hence the divide at Santa Cruz del Quiché, like that at Guatemala City, evidently provided passage either way and at different times. It is difficult to say which species crossed first without knowledge of the relative ages of each species. In the absence of a known fossil record for *Profundulus,* the interpretation as to which species group is more primitive must rest largely upon morphological considerations. Most of the characters listed for the *labialis* group (Table II, p. 19) may be interpreted as more specialized than those of the *punctatus* group: thus the preorbital is naked (rather than scaled), the scales (and vertebrae) are more numerous, the anal fin of the female is more modified, and the morphology of the mouth parts indicates more specialized feeding habits (a browsing type rather than an omnivorous feeder).

For these reasons I hypothesize that *P. guatemalensis* (or its ancestral form) was the first species of *Profundulus* to enter the Negro basin; that *labialis* enter subsequently from the Río de Chiapa basin and then later gained access to the Motagua basin. If these assumptions are correct, it becomes necessary to offer an explanation for the apparent difference in relative abundance of these two species in the Negro system. If *guatemalensis* became established there first and it is the more generalized species, how is it that *labialis* was able to invade the same waters and apparently become dominant? The answer evidently involves an appraisal of the ecological requirements of the two species, but there is also need for further collecting to determine if *labialis* is really more common. A detailed account of the ecology of *Profundulus* is intended for publication elsewhere, and only a summary of the more important data on *guatemalensis* and *labialis* is presented here. The precise habitat of the two species is notably different when they occur together and is influenced by stream gradient, depth of water, and the nature of the bottom.

The species were taken together in the Motagua system (once) and in the Negro basin (3 times); at all but one of these places the streams were rocky, consisting of about 60 to 70 per cent boulders and rubble. In such situations, *P. labialis* preferred the riffles and *P. guatemalensis* the pools. At the Río Rabinal west of Rabinal (Negro system), 119 *labialis* and 4 *guatemalensis* were seined. Here the stream was of low gradient, shallow and sandy (90 per cent sand, 10 per cent rubble and gravel), with occasional short, rocky riffles, few pools, and some undercut banks. The scarcity of *guatemalensis* was presumably due to the poor development of pools; the individuals taken obviously represented stragglers, presumably from above. Only about 2 miles upstream the habitat changes greatly, for here the Río Rabinal runs in a shaded mountain canyon with an estimated bottom composition of 60 per cent boulders, 15 per cent rubble, 5 per cent gravel and only 20 per cent sand (Holloway, 1950: Table 3, items 43-44). Although *Profundulus* was seen, no collection was made, but I feel confident that further collecting will show that the population of *Profundulus* here is dominated by *P. guatemalensis*. At San Jerónimo, where 4 *labialis* and 80 *guatemalensis* were obtained with rotenone, the Río San Jerónimo is more like the upper Río Rabinal, with long, bouldery riffles and pools, and a bottom composition estimated at 30 per cent boulders, 30 per cent rubble, 15 per cent gravel, and 25 per cent sand (Holloway, 1950: Table 3, item 46). Consequently, it was not unexpected that *guatemalensis* predominated. Further collecting in the headwater regions of other tributaries of the Río Negro would undoubtedly extend the known range of *P. guatemalensis* in that drainage system, although it seems clear that *P. labialis* does live at higher elevations than *guatemalensis*, at least in the basin of the Río Negro. Our present knowledge of the distribution of the two species in the Motagua and Negro systems is too scant to warrant making definite statements about their comparative abundance.

Geologically speaking, Middle America is a structural unit that is independent from either North or South America. As Schuchert (1935: 314-43) and Sapper (1937: 1-10) have indicated, much of its mountainous region is composed of rocks of Paleozoic to Mesozoic age. The isthmus that now connects North and South America was split by successive water gaps into a series of islands during the Tertiary (see Fig. 1 in Mayr, 1946). Thus, South America was separated from North America during the greater part of Tertiary time. A land connection bridging the continents probably did not exist between the Lower Eocene and Upper Pliocene epochs.

The mountain mass of southern Chiapas and western Guatemala has had a continued existence above sea level throughout a major portion of geological time. Hence, as Griscom (1932: 28) has pointed out, these highland areas have been available as a refuge for plant and animal life that has been driven out of the lowland areas by intermittent marine floodings. It is in these long-isolated uplands that *Profundulus* evidently originated and underwent early differentiation, probably during the existence of the Tehuantepec water gap sometime between middle Miocene and early Pliocene times. It was during this period that southern Chiapas was cut off from the remainder of México. The origin of *Profundulus* is thus believed to have taken place at least as early as Pliocene time and probably dates back to the Miocene. This genus takes its place among other genera of fishes, reptiles, birds and mammals that represent endemics of a true Middle American fauna (Gadow, 1916: 545; Myers, 1938: 350-51; discussion and references by Mayr, 1946: 10, and Simpson, 1950: 383-89; Stuart, 1951: 27-33; 1954: 28-30).

SUMMARY

This study of the systematics of the cyprinodontid fish genus *Profundulus* is based upon a morphological examination of 9,280 specimens, an analysis of the habits, habitat and ecology of the species, and a consideration of the effect of recent hydrographic changes on interspecific competition and on the dispersal and origin of the species. Although belonging to a family, the Cyprinodontidae, that tolerates wide fluctuations in salinity, this genus is known only from fresh water. Whether it has been wholly confined to fresh water during the history of its dispersal is problematical.

Five species of *Profundulus*, all illustrated, are recognized and are assigned to two distinct species groups. The *punctatus* group (subgenus *Profundulus*) includes *punctatus* and *guatemalensis*, two very closely related, allopatric species. The *labialis* group (subgenus *Tlaloc*) includes *labialis*, *candalarius*, and *hildebrandi*, of which the second is a geographic segregate of *labialis*, whereas *hildebrandi*, isolated atop the highest mountain mass of Chiapas, is believed to represent a much earlier evolutionary stage.

The recognition of *Profundulus* as a genus distinct from *Fundulus*, its closest relative, is substantiated by an appraisal of the characteristics used to distinguish all species of both genera. Two new taxonomic characters for separating these genera — the form of the premaxillary process and the structure of the median hypural bone — were discovered in the present study.

Profundulus is distributed over both slopes of Middle America (Map 1), from southern México to Honduras, as follows: *P. punctatus* occurs on the Pacific versant from the Río Papagayo of Guerrero, México, nearly to El Salvador; and on the Atlantic slope from the Isthmus of Tehuantepec (Río Coatzacoalcos) eastward into the basin of the Río de Chiapa of Chiapas, México. *P. guatemalensis* is found in Pacific streams of the highlands of Guatemala, El Salvador, and western Honduras (Río Lempa), and in upper parts of the Río Motagua and Río Negro (both Atlantic) drainages of Guatemala. *P. labialis* is almost confined to the Atlantic drainage of southern Chiapas (Río de Chiapa, Río Jatatė) and Guatemala (Río Negro, Río Polochic, Río Motagua), but is known also from two streams of the Pacific slope and from

Lake Atitlán, Guatemala (introduced into the latter). *P. candalarius* is known only from the hydrographically isolated Río Grande de Comitán in Chiapas, México, and from a limestone spring at Candalaria, Guatemala. *P. hildebrandi* is confined to an isolated limestone plateau near San Cristóbal de Las Casas, Chiapas, México. The species typically inhabit mountain streams at elevations between 2,000 and 8,000 feet, although *P. punctatus* descends to as low as 300 to 400 feet on the Pacific coastal plain of México (Chiapas) and Guatemala.

The species of *Profundulus,* like those of the salmonoid fishes, are remarkably variable, with the result that most of them have evolved into a bewildering array of local populations that defy orderly taxonomic arrangement. The systematist is thus faced with the alternative of naming many local populations or of recognizing a few highly variable taxa. Through the study of many specimens scattered throughout the range of the genus it has been possible to draw the species lines more clearly and to delimit populations on the basis of broad similarities rather than to overemphasize local differences. For these reasons and because of the random nature of the variations, I have refrained from naming any new taxonomic units even though some borderline populations might be worthy of recognition. The precise status of such populations remains to be determined.

Some or all of the type specimens, or topotypes, of the described species of *Profundulus* were examined. Lectotypes of *P. guatemalensis* and *P. labialis* are designated. The nominal species *P. pachycephalus* (Günther), *P. oaxacae* (Meek), and *P. scapularis* Fowler are synonymized with *P. punctatus,* and *P. balsanus* Ahl is tentatively so treated. The tribe Profundulini (Profundulidi) of Hoedeman and Bronner (1951) is shown to be an unnatural group, with the suggestion that it be abandoned. The genus *Tlaloc* described by Alvarez and Carranza (1951), as a member of the Rivulini, is shown to have been placed in the wrong tribe and is synonymized with *Profundulus.*

A diagnosis of *Profundulus* is given, followed by a key to the species. No unquestioned fossil material of this genus has been described, although the suggestion is made that it cannot be certain whether some North American Pliocene fossils referred to *Fundulus* may not belong to *Profundulus.* The two observed osteological differences between the genera, mentioned above, may be helpful in this connection.

A detailed discussion of variation within *P. punctatus, P. guatemalensis* and, particularly, *P. labialis* is presented; the material at hand of *P. candalarius* is insufficient for a critical analysis of variation. *P. hildebrandi* is represented by two samples from one locality.

The origin and evolution of each species group is discussed. It is postulated that the *punctatus* group is the more primitive, with *guatemalensis* the most generalized species, and that this group arose in the southern highlands of Guatemala; it is thought that the *labialis* group, with one widespread species, arose in the highlands of Chiapas, México. The two groups were subsequently brought into contact in widely separated areas through complex hydrographic changes. Eight possible or probable migration routes are described in the section on Distribution and Origin.

The ecology of *P. guatemalensis* and *P. labialis* in the Río Motagua and Río Negro, Guatemala, where they coexist, is briefly outlined. A more detailed treatment of the ecology of *Profundulus* is in preparation. Differences, perhaps in their behavioral patterns but certainly in the ecological niches favored by *guatemalensis* and *labialis,* permit them to live side by side, although each species is thought to be more abundant in the headwater and in the lower portions, respectively, of many of the streams where they occur together. More field work is needed to verify this belief.

Geologically, Central America is not a structural part of either North or South America, but rather represents a third element between those two. Much of the mountainous region of Guatemala is Paleozoic (and most of that of Chiapas is Mesozoic) and has had a continued existence above sea level since then. In contrast, the Pacific lowlands of Guatemala and southern México comprise Pleistocene and Recent deposits. Consequently, the highlands have always provided a refuge area for faunas and floras expelled from the lowlands by repeated marine invasions.

The origin and differentiation of *Profundulus* evidently occurred in these long-isolated highland areas, presumably at a time when the Tehuantepec water gap (late Miocene to middle Pliocene) effectively cut off the mountain regions of Central America (including the Chiapas highlands) from the remainder of México. The evolution of this genus thus probably dates back at least to the Pliocene and likely to the Miocene. *Profundulus* is one of the distinctive elements of the endemic fauna of Middle America.

MATERIAL EXAMINED

Profundulus punctatus

Pacific drainage, Guatemala. — USNM 134626 (20), trib. Río Michatoya (estimated elevation, 700 ft.) about 7 mi. SE of Escuintla on road to Chiquimulilla; USNM 134627 (10), trib. Río Chiquimulilla (825 ft.) about 3 km. W of Chiquimulilla; USNM 144384 (27), Río Aceituno (580 ft.) 8.2 mi. W of Escuintla on military highway; USNM 144385 (4) and 144392 (42) and UMMZ 166695 (16), Río Colojate (515 ft.) 4 km. SW of La Democracia (12 airline mi. SE of Escuintla); USNM 144386 (31), trib. Río Madre Vieja (1300 ft.) 4 mi. N of Patulul on road to Mazatenango; ANSP 64137 (holotype of *P. scapularis*) and 64242-70 (29 paratypes), Río Bravo, Finca Mocá (3000 ft.) at base of Volcan de Atitlán; ANSP 64138-47 (10 paratypes of *P. scapularis*[1]), USNM 144388 (27 topotypes) and UMMZ 166692 (15 topotypes), Lago Mocá at Finca Mocá at base of Volcan de Atitlán near source of Río Bravo; USNM 144389 (145) and UMMZ 166693 (60), Río Camaya (1360 ft.), trib. Río Tulate, about 5 mi. W of Mazatenango on military highway; USNM 144387 (12), Río Naranjo (400 ft.) above bridge of military highway just E of Pajapita; USNM 144383 (19), Río Gramal (825 ft.?) about 6 mi. S of Malacatán on road to Ayutla; CNHM 5552 (7), Mazatenango (1260 ft.); CNHM 5541 (2), San José de Idolo (600 ft.); S of Mazatenango; USNM 147744 (62), Yepocapa (3500 ft.); 18 airline mi. ESE of Antigua; USNM 94217 (2), Finca del Rosario (3300 ft.) 6

[1]In the original description (Fowler, 1936: 522) it is stated that these specimens were taken with the holotype, but the data in the jar contradict this.

airline mi. SW of Yepocapa; USNM 127088 (19) and UMMZ 166702 (6), Lake Atitlán (5100 ft.); UMMZ 144336 (15), Río Guacalate (350 ft.?) between Mixtan and Santa Maria, about 7 mi. S of Escuintla; UMMZ 158448 (1), gorge (4225 ft.) 1 km. S of Yepocapa; UMMZ 158447 (7), trib. Río Madre Vieja (3800 ft.) at Finca Santo Tomás, 3 mi. S of SE arm of Lake Atitlán; UMMZ 158444 (5) and 159904-5 (61) and USNM 162739 (7), Finca La Paz (3930 ft.) in basin of Río Naranjo, 9 airline mi. S of San Marcos; and BM 1864.1.26. 187A-D (4, first 3 cotypes of *F. pachycephalus*), Lake Atitlán (5100 ft.).

Pacific drainage, México. — The following localities are in Chiapas: USNM 86197 (1), Tapachula (600 ft.); UMMZ 166661-2 and 166665 (6), Finca Esperanza (650 ft.) 6 km. NW of Escuintla; UMMZ 166664 (1), Río Cacaluta (650 ft.) near Finca Esperanza; UMMZ 166663 (1), trib. Río de Chiapa (2600 ft.) on road summit between Arriaga and Cintalapa; UMMZ 166669 (5), Río Montebonito (300 ft.) 2 km. W of Arriaga; UMMZ 166668 (29), Río Montebonito (2500 ft.?) 15 mi. N of Arriaga. The following are in Oaxaca: USNM 144420 (4, poor condition), Tehuantepec (150 ft., no *Profundulus* taken here recently); BM 1906.6.1.331-38 (8), Río Tequisistlán at Tequisistlán (600 ft.), trib. Río Tehuantepec, 25 airline mi. ENE of Tehuantepec; BM 1906.6.1.339-42A, B (5), Río Totolopán at Totolopán (4000 ft.), trib. Río Tehuantepec, 39 airline mi. SE of Oaxaca; CNHM 3721 (holotype of *F. oaxacae*), 3722 (38, paratypes), SNHM 31927 (4, paratypes), and UMMZ 65219 (1, paratype), Río Verde at Oaxaca (5000 ft.). The following are in Guerrero: UMMZ 157291 (2, paratypes of *P. balsanus*), Malinaltepec (6500 ft.) about 40 airline mi. E of Acapulco (see text); and UMMZ 108595 (56), Río Papagayo (1300 ft.?) at highway crossing 32 mi. by road N of Acapulco.

Atlantic drainage, México. — USNM 131686 (17, poor condition), Río Grande de Chiapa at Tuxtla Gutiérrez (1800 ft.), Chiapas; UMMZ 166666 (5), Río Chico at Chiapa (1800 ft.), Chiapas; USNM 162741 (2), Río de las Cruces at Las Cruces (2100 ft.), Chiapas; UMMZ 166667 (2), Río Ortis Rubio (ca. 2250 ft.; Río de la Venta system) near Ortis Rubio [= Cortiz Rubio] between Las Cruces and Arriaga, Chiapas; USNM 132267 (34), Piedra Parada (3600 ft.) 22 mi. W of Tuxtla Gutiérrez, Chiapas; UMMZ 161522 (8), trib. Río Coatzacoalcos (975 ft.) at Santa María (or Chimalapa), Oaxaca; and BM 1890. 10.10.21 (1), Santo Domingo de Gúzman (900 ft.) (Buller, coll.), in Atlantic drainage of Oaxaca (see text).

Profundulus guatemalensis

Pacific drainage, Guatemala. — USNM 134600 (103) and UMMZ 166691 (113), Río de las Vacas (4450 ft.) 6 mi. S of Guatemala City; USNM 134601 (2), Lake Calderas (5860 ft.) 11 km. S of Lake Amatitlán; USNM 134602 (87), Río del Rosario at Finca El Rosario (3000 ft.?), trib. Río Aguacapa, 6 airline mi. SE of SE corner of Lake Amatitlán; UMMZ 166677 (91), trib. Río Aguacapa (2800 ft.?) about 3 mi. W of Laguna del Pino (45 km. SSE Guatemala City); USNM 134604 (39), Río Las Cañas (2900 ft.?) about 3 mi. W of Santa Rosa (8 airline mi. N Cuilapa); USNM 134605 (105), Río Quebrada Tasagera (2900 ft.?), about 1 mi. W of Santa Rosa; USNM 134606 (31), Río Escalante at Santa Rosa (2900 ft.?); USNM 134607 (2), trib. Río Escalante

(3050 ft.?) just below Casillas (NW Santa Rosa); UMMZ 166678 (15), Río Los Esclavos (2900 ft.?) just SE of Cuilapa; USNM 134609 (171) and UMMZ 166697 (189), trib. Río de Paz at San Diego (2950 ft.), on Pan-American Highway 7 mi. W of Jutiapa; USNM 134610 (24), trib. Río de Paz at Amayita (2850 ft.), on Pan-American Highway 4 mi. W of Jutiapa; USNM 134611 (3), Río Villalobos (4150 ft.) 100-400 yds. above Lake Amatitlán; USNM 134618 (29), spring outlet at El Cubo (4500 ft.?), trib. Río Guacalate, 1.5 mi. SE of Antigua; USNM 134619 (227) and UMMZ 166680 (63), Río Guacalate (4500 ft.?) 1 mi. SE of Antigua (topotypes); USNM 134620 (421) and UMMZ 166681 (140), springs and ditches at Apocentos (5550 ft.?) about 1 mi. S of Chimaltenango; ANSP 64722-33 (12), El Zapote (3000 ft.?), trib. Río Guacalate, 7.5 airline mi. NW of Escuintla; USNM 134624 (235) and UMMZ 166683 (100), trib. Río Aguacapa (4000 ft.?), on Pan-American Highway 38 km. SSE of Guatemala City; USNM 134625 and 144411 (93) and UMMZ 166684 (44), Laguna del Pino (3400 ft.), about 48 km. SSE of Guatemala City; USNM 134628 (135) and UMMZ 166685 (5), trib. Río Los Esclavos near Prado (2000 ft.?), 6 airline mi. SSW of Cuilapa; USNM 134630 (87), trib. Río Los Esclavos (2025 ft.?) about 4.5 airline mi. SSW of Cuilapa; USNM 134631 (88), trib. Río Aguacapa and Río Aguacapa (3000 ft.?) about 4 mi. W of Laguna del Pino; USNM 144400 (43) and UMMZ 166696 (14), trib. Río Michatoya (1750 ft.) about 3.5 mi. N of Escuintla; USNM 144399 (39), trib. Río Michatoya (3800 ft.), 1 km. S of Palín, 7 airline mi. SW of Amatitlán; USNM 144410 (64), Río Michatoya (3500 ft.) about 2 km. below Palín; USNM 144409 (31) and UMMZ 166700 (10), Río Atulapa (3000 ft.), trib. Río Olopa (Río Lempa system), about 2 mi. SE of Esquipulas; USNM 144402 (267, poor condition), Lake Ayarza (4700 ft.; interior drainage), 17 airline mi. NW of Jutiapa; USNM 144406 (220), trib. Río Los Esclavos, at San Rafael Las Flores (4400 ft.), 4 mi. S of Mataquescuintla; USNM 37393 (1), Amatitlán (4150 ft.); UMMZ 158449-50 (8), trib. Río Los Esclavos at and near Finca La Gloria (1600 ft.), 13 km. ENE of Chiquimulilla; and UMMZ 144654 (3), Santa Catarina de Pinula (ca. 5200 ft.; Lake Amatitlán drainage), about 5 mi. SE of Guatemala City.

Pacific drainage, El Salvador and Honduras. — USNM 87231 and CNHM 12050 (20), Río del Molino (2000 ft.?), trib. Río de Paz, near Ahuachapán, El Salvador; UMMZ 166703 (4), El Río del Pueblo Viejo at Intibucá (4000 ft.?), Dpto. Intibucá, trib. Río Lempa, Honduras; and UMMZ 113398 (1), trib. Río Choluteca, Tegucigalpa, Honduras (locality erroneous; see text).

Atlantic drainage, Guatemala. — USNM 134621 (1), trib. Río Motagua (3800 ft.?) below Chinautla, about 6 mi. N of Guatemala City; USNM 134622 (46), trib. Río Motagua (3800 ft.?), 1 mi. below San Antonio Las Flores, about 8 mi. N of Guatemala City; USNM 134617 (146), trib. Río de las Vacas (4200 ft.?; Motagua system), 1 km. NW of San Antonio Las Flores; UMMZ 166682 (33) and USNM 144397 (226), trib. Río de las Vacas (4700 ft.; Motagua system), just above railroad bridge about 3 mi. N of Guatemala City; USNM 144395 (112) and UMMZ 166694 (40), trib. Río Motagua (5300 ft.) about 2 mi. NNW of San José de Pinula (9 airline mi. SE Guatemala City); UMMZ 158445 (3), trib. Río de las Vacas (6560 ft.; Motagua system), 2 km. N of Granaja Los Ocales (about 4 km. W San José de Pinula); USNM 144393 (126), trib. Río Purgatorio (3000 ft.; Motagua system) near San Antonio La Paz, 24 mi. NE of Guatemala City on road to El Rancho; USNM 144403 (6), Río Morazán (ca. 2000 ft.; Motagua system) at road crossing just E of Morazán (10 airline mi. NNW El Rancho); USNM 134613 (14), trib. Río Motagua just S of Granados (ca. 3000 ft.; 22 airline mi. N Guatemala City); USNM 144405 (120) and UMMZ 166701 (50), trib. Río Puerta Abajo (ca. 6700 ft.; Motagua system), 4 mi. W of Chimaltenango; USNM 134615 (4), Río Rabinal (3000 ft.; Negro system) about 1 mi. N of Rabinal; USNM 134633 (55) and UMMZ 166686 (25), Río San Jerónimo at San Jerónimo (3350 ft.); and USNM 144394 (46), Río Carchelá (4300 ft.; Negro system) about 18 mi. N of Salamá on road to Cobán.

Profundulus labialis

Pacific drainage, Guatemala (see Map 3). — USNM 144404 (14), trib. of Río Madre Vieja (6150 ft.) E of Lake Atitlán; UMMZ 158446 (45), Río Molino (6175 ft.), trib. Río Madre Vieja, at km. 82 on road between Lake Atitlán and Chimaltenango; ANSP 64747-79 (33), Río Chajic, trib. Río Madre Vieja, at Tecpán (7500 ft.); USNM 134641 (80), Río Panajachél (5110 ft.), trib. to Lake Atitlán, at and above highway bridge SE of Panajachél; and USNM 134645 (245) and UMMZ 166690 (94), Río Samalá (ca. 8000 ft.) about 2 to 3 mi. W of Totonicapán.

Atlantic drainage, Guatemala. — USNM 134612 (38) and UMMZ 166679 (12), Río Motagua at Concuá (ca. 2300 ft.) about 20 airline mi. N of Guatemala City; USNM 134614 (10), trib. Río Motagua (ca. 3000 ft.) just S of Granados (just NE Concuá); USNM 134640 (142), Río Grande (Motagua) at road crossing (ca. 6600 ft.) 1 km. NNW of Chichicastenango; USNM 144396 (97), Lake Lemoa (6700 ft.; interior basin), 7.5 mi. S of Santa Cruz Quiché; USNM 134616 (119), Río Rabinal (ca. 3000 ft.; Negro system) about 1 mi. N of Rabinal; USNM 134632 (4, topotypes of *F. labialis*), Río San Jerónimo (Negro system) at San Jerónimo (3350 ft.); USNM 134634 (96) and UMMZ 166687 (47), Río Salamá (Negro system) at Salamá (3100 ft.); USNM 144398 (182) and UMMZ 166698 (60), Río Carchelá (4300 ft.; Negro system) 18 mi. N of Salamá on road to Cobán; USNM 134638 (101), Río Cholá (Negro system), 1 km. E of San Miguel Uspantán (6000 ft.) on road from Cobán to Sacapulas; USNM 134639 (93), Río Negro at Sacapulas (4500 ft.); USNM 134643 (258), Río Aguacatán (Negro system) at Aguacatán (5580 ft.), 11 airline mi. E of Huehuetenango; USNM 134644 (151), pond (ca. 7260 ft.; Negro system) about 3 mi. ENE of Huehuetenango on road to Sacapulas; USNM 144390 (72), headwaters of Río Negro (6700 ft.), 6 mi. WSW of Santa Cruz Quiché on road to Totonicapán; USNM 144391 (43), Río Momostenango (6700 ft.; Negro system) about 2 mi. N of Momostenango; UMMZ 131140 (1), Río Negro at La Primavera (ca. 2300 ft.; near Chixoy), 16 airline mi. SW of Cobán on road to Sacapulas; UMMZ 131145 (30), trib. Río Negro near La Primavera (ca. 4100 ft.; see above); BM 1864.1.26.192A (lectotype of *F. labialis*) and 192B-D (3 paratypes) and 1864.1.26.184A-C (3 topotypes), Río San Jerónimo at or near San Jerónimo (3350 ft.); BM 1861.8.12.18-19 (2 paratypes) and 1869.2.23.11A-B (2), Río Chixoy (Negro) (originally listed only as Guatemala); USNM 134635 (60) and UMMZ 166688 (29), headwaters of Río Polochic (4000-5000 ft.), from 1 km. to 5 mi. W of Tamahú; USNM 134636 (145), Río Panimá (Polochic system) at Purulhá (ca. 5200 ft.), 16 airline mi. SE of Cobán; USNM 134637 (229), Río Santa Lucia (ca. 5100 ft.), headwaters of Río Cahabón (Polochic system), 2.5 km. N of Patal, 13 airline mi. SE of Cobán; USNM 112281 (20) and 144408 (69) and UMMZ 166699 (30), Lake San Cristóbal (ca. 4300 ft.) and its tributary (Polochic system) at San Cristóbal, 8 airline mi. SSW of Cobán; ANSP 64922-27, brooks near San Cristóbal (2) and brook between San Cristóbal and Santa Cruz (1); USNM 144407 (21), Río Chicoy (Polochic system) at San Pedro Carchá (4300 ft.), about 3 mi. E of Cobán; UMMZ 131147-48 (63), Finca Chichén (4753 ft.; Polochic system) about 10 km. S of Cobán; UMMZ 105456 and 131825 (13), Río Pansamalá (4125 ft.; Polochic system) about 35 km. E of Cobán; USNM 134642 (46) and UMMZ 166689 (22), Río Saleguá (ca. 6000 ft.; Río de Chiapa system), about 1 mi. W of San Sebastian (ca. 9 airline mi. WNW Huehuetenango); and UMMZ 159909 (74), Río Canibal (4300 ft.), trib. Río Cuilco (Chiapa system), about 5 airline mi. E of Cuilco.

Atlantic drainage, México. — The following are in the basin of the Río de Chiapa, Chiapas: UMMZ 144439 (1), Prussia (ca. 4250 ft.) 30 airline mi. NNW of Escuintla; UMMZ 157639 (10), trib. Río de Chiapa (2000 ft.?) 2-3 mi. E of Aztlán (between Chiapa de Corzo and Ixtapa on road to Las Casas); UMMZ 157641 (37), trib. Río de Chiapa (2000 ft.?) 2-3 mi. W of Aztlán; UMMZ 157644 (17), spring (ca. 1400 ft.) 4 km. S of Chiapa de Corzo; UMMZ 167057 (64), Río Chico (ca. 1400 ft.) at eastern limits of Chiapa de Corzo; UMMZ 167059 (20) and USNM 163552 (7), Río Salado (ca. 1900 ft.) 1-2 km. from Chapilla (30 mi. SE Tuxtla Gutiérrez); USNM 163548 (2) and 163553 (1), Río Sabinal (1800 ft.) 1/4 mi. W of Tuxtla Gutiérrez; UMMZ 167056 (2), Arroyo San Fernando (1850 ft.?) at San Fernando, about 10 mi. NW of Tuxtla; USNM 163549 (21), Rancho Cahuaré Springs (ca. 1400 ft.), 3 mi. E of Chiapa de Corzo; USNM 163550 (2), Río Nandayapa, 14 leagues from [SE of?] Chiapa; USNM 163551 (21), small laguna of Río Frio, 1/4 mi. from its mouth in Río Grijalva (or Chiapa); UMMZ 167058 (3), Río Grijalva (ca. 1450 ft.) between Chiapa de Corzo and Acala; UMMZ 166676 (4), Río Trapiche (1500 ft.?), 5 leagues from Chiapa de Corzo; UMMZ 167060 (92), Río de las Flores at Paso Chiapa (1700 ft.; on highway from Tuxtla to Arriaga); UMMZ 167061 (3), Río de las Flores, between Cintalapa and Palo Grande; UMMZ 167062 (6), Río Ortis Rubio (2250 ft.?), trib. Río Cintalapa (trib. Río de las Flores), near Ortis Rubio [= Cortiz Rubio] at Puente Las Manquitos, on road between Las Cruces and Arriaga; and UMMZ 166675 (2), small stream at Santa Elena (ca. 6000 ft.), just E of Amantenango (on road between Las Casas and Comitán). The following 2 collections, also from Chiapas, are in the basin of the Río Usumacinta: UMMZ 161767 (1), trib. Río Santa Cruz (trib. Río Jataté) at El Real (ca. 2100 ft.), 23 airline mi. ENE of Ocosingo; and UMMZ 162154 (2, paratypes of *Tlaloc mexicanus*), Arroyo San Francisco (trib. Río Jataté) at Ocosingo (ca. 2650 ft.).

Profundulus candalarius

Interior drainage, México. — The following collections, at elevations between 5000 and 5200 feet, are from the basin of the Río Grande de Comitán in south-central Chiapas: UMMZ 166670 (8), main river at Yocnajab, about 15 km. E of Comitán; UMMZ 166671 (23), main river at Santo Tomás, about 20 km. ESE of Comitán; UMMZ 166672 (28), Arroyo San José del Arco, about 4 km. SE of Santo Tomás; UMMZ 166673 (36) and USNM 162745 (12), La Ciénega, an overflow of the river 1 km. NE of Comitán; and UMMZ 166674 (166), main river 1.5 km. E of Comitán.

Guatemala. — CNHM 9071 (holotype) and 9072 (allotype), limestone spring at Candalaria (ca. 3300 ft.), near the Mexican boundary, 6 leagues from Nentón; reportedly in the Río de Chiapa basin (but see text).

Profundulus hildebrandi

Chiapas, México. — UMMZ 157633 (holotype) and 157634 (485, paratypes), Laguna de María Eugénia (7260 ft.), San Cristóbal de las Casas, about 32 airline mi. E of Tuxtla Gutiérrez; and UMMZ 157652 (30, paratypes), from the same locality.

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PLATES

PLATES I–IX

PLATE I

Profundulus punctatus

Small adults and young from the Pacific drainage of Guatemala (A–E) and Chiapas, México (F). For localities, see Maps 1–2.

A. Mature male, 40 mm. S.L., USNM 134626, 7 miles SE of Escuintla.

B. Mature male, 39 mm., UMMZ 159905, Finca La Paz.

C. Mature male, 36 mm., UMMZ 166693, Río Camaya, about 5 miles W of Mazatenango.

D. Immature female, 31 mm., UMMZ 159905, Finca La Paz.

E. Immature male, 30 mm., UMMZ 166693, Río Camaya.

F. Mature female, 29 mm., UMMZ 166668, Río Montebonito.

Specimens A, D, and E were selected to show atypical weak or obsolete brown spotting on sides. Photographs by Photographic Services.

PLATE I

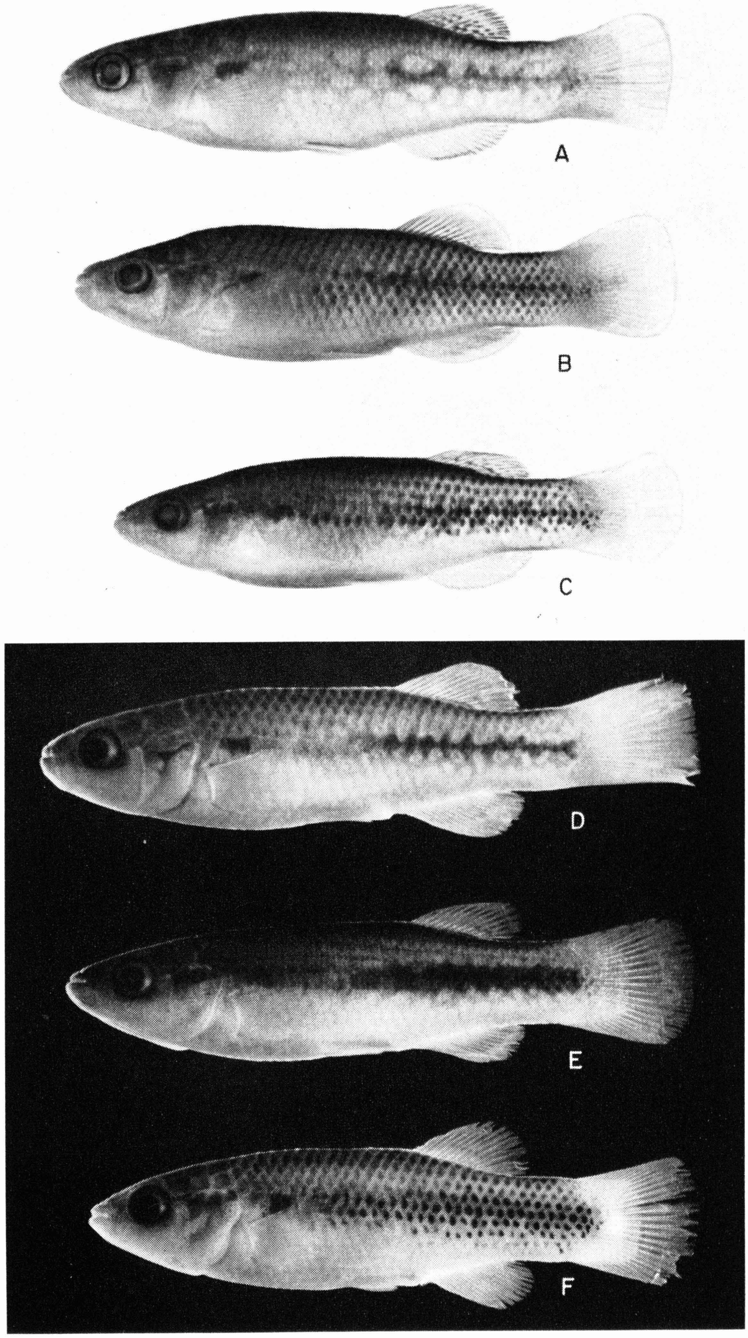


PLATE II

Three species of *Profundulus* from Guatemala

See Map 2 for localities.

A. Radiograph of lectotype (see text) of *P. guatemalensis,* 64 mm., from Río Guacalate, probably near Dueñas.

B. Radiograph of topotype of *P. guatemalensis,* 61 mm., UMMZ 166680, Río Guacalate 1 mile SE of Antigua.

C. Radiograph of lectotype (see text) of *P. labialis,* 99 mm., from San Jerónimo.

D. Male of *P. punctatus,* 51 mm., UMMZ 166695, Río Colojate, 4 km. SW of La Democracia.

E. Female, *P. punctatus,* 47 mm., Finca Mocá (Map 3).

Radiographs by author, retouched by W. L. Brudon. Photographs by Photographic Services.

PLATE II

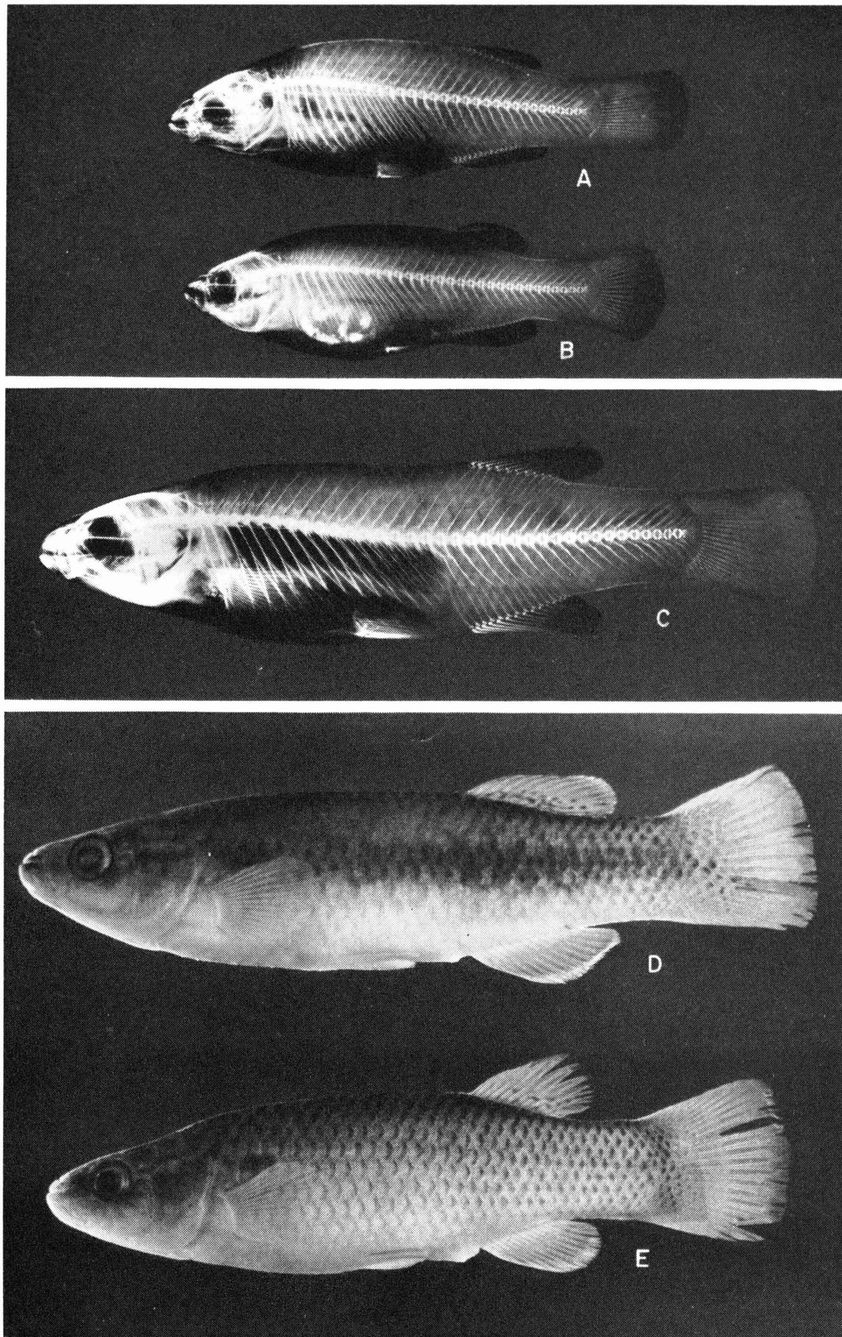


PLATE III

Profundulus guatemalensis

Adults from the Pacific (A–B) and Atlantic (C–D) drainages of Guatemala. For localities, see Map 2.

A. Topotypic male, 62 mm., UMMZ 166680, Río Guacalate 1 mile SE of Antigua.

B. Topotypic female, 63 mm., with same data.

C. Male, 44 mm., USNM 144394, Rio Carchelá 18 miles by road N of Salamá.

D. Female, 44 mm., with identical data.

Photographs by Photographic Services.

PLATE III

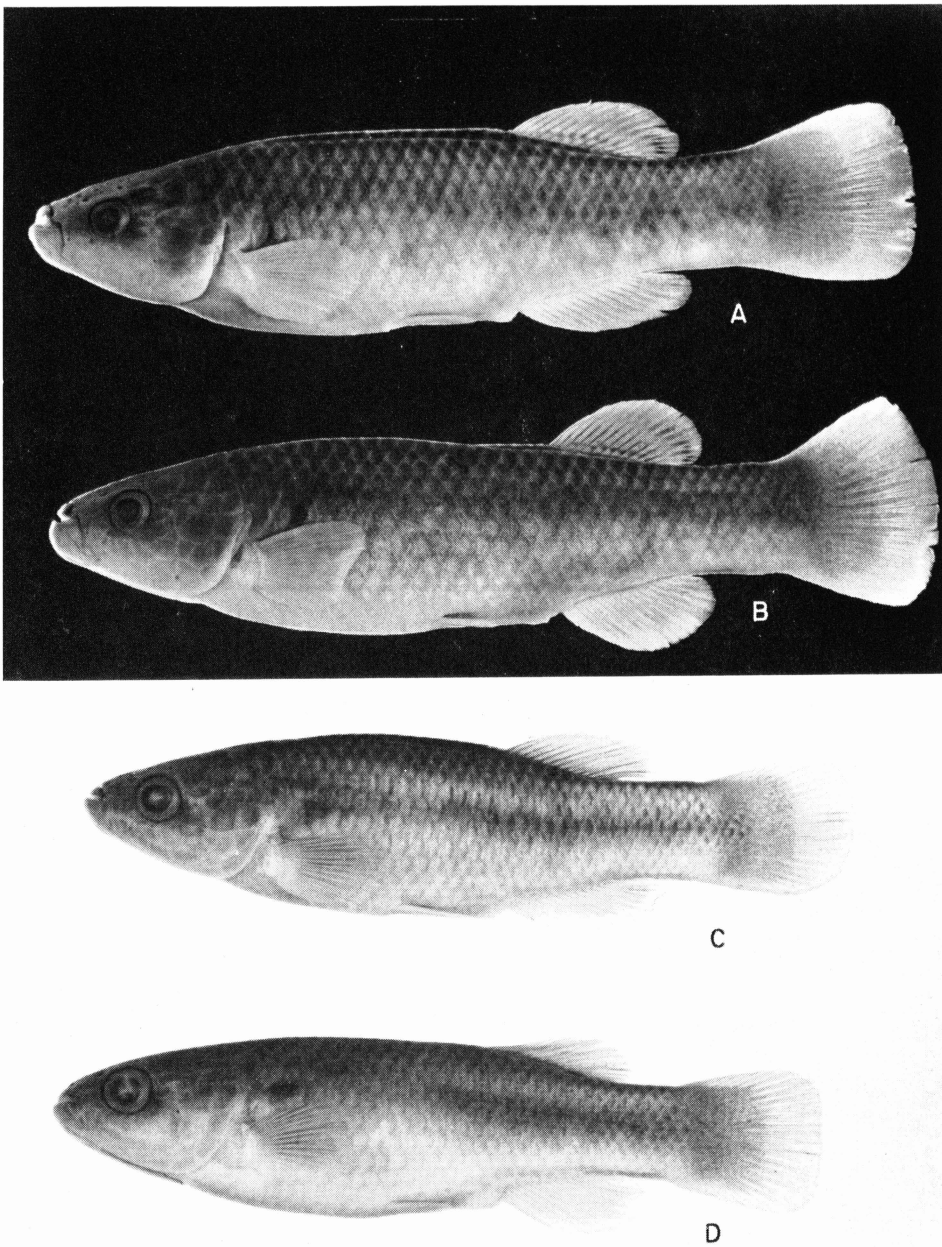


PLATE IV

Profundulus guatemalensis

Small to large adults and an immature specimen from Aposentos, 1 mile S of Chimaltenango (Map 2), in the Pacific drainage of Guatemala.

A. Old male, 74 mm., USNM 134620; photograph by Smithsonian Institution.

B. Nuptial male, 43.5 mm., UMMZ 166681.

C. Mature female, 37 mm., same data.

D. Nuptial male, 35 mm., same data.

E. Immature female, 26 mm., same data.

Specimens B–E photographed by Photographic Services.

PLATE IV

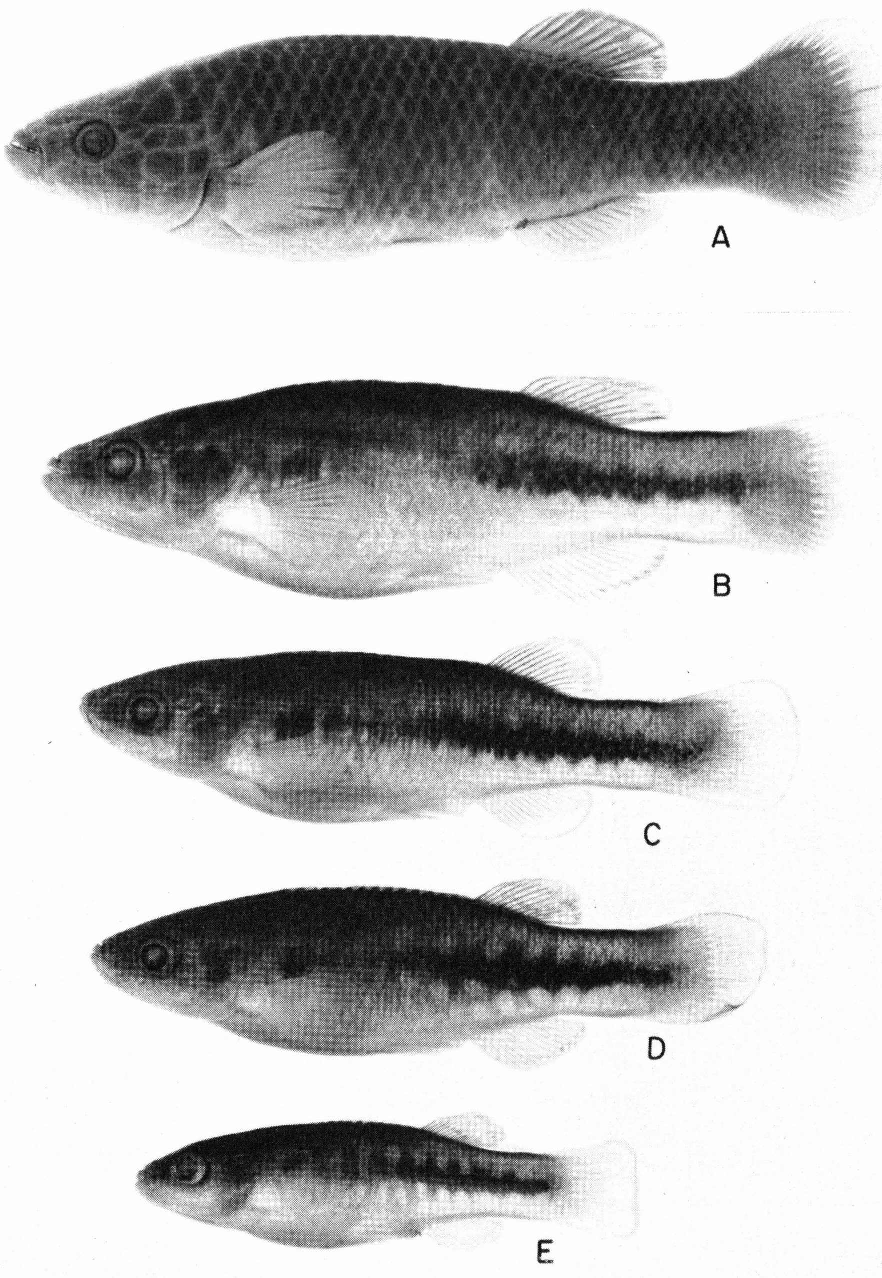


PLATE V

Types of *Profundulus hildebrandi*

Above: Holotype, nuptial male, 66.5 mm., UMMZ 157633, Laguna María Eugénia, San Cristóbal de las Casas, Chiapas, México (Map 1).

Below: Paratopotype, female, 67 mm., UMMZ 157634, taken with the holotype.

Photographs by Photographic Services.

PLATE V

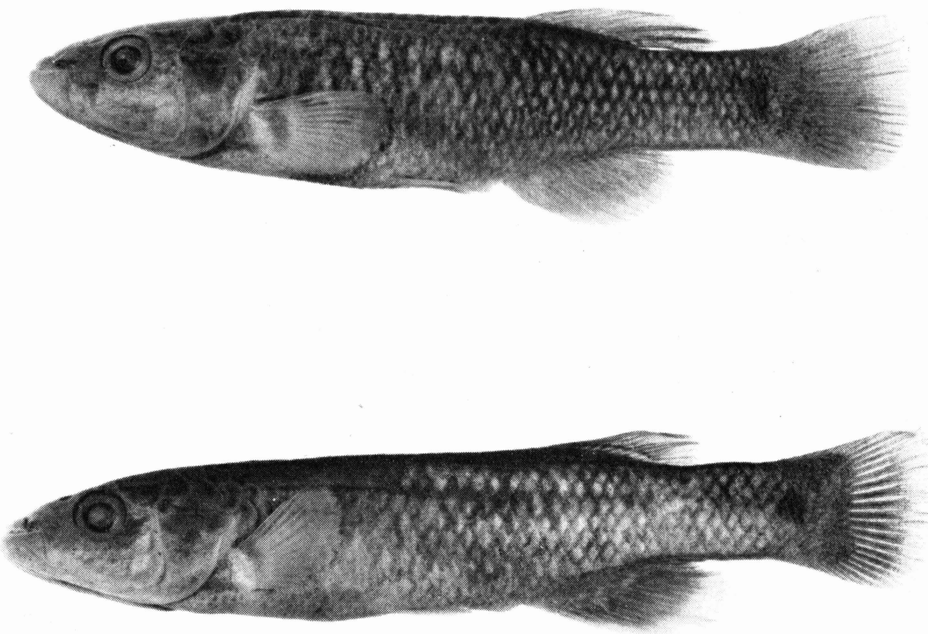


PLATE VI

Paratopotypes of *Profundulus hildebrandi*

A. Mature male, 40 mm.

B. Mature female, 40 mm.

C. Immature, 33 mm.

D. Immature, 29 mm.

All are UMMZ 157634, Laguna María Eugénia, San Cristóbal de las Casas, Chiapas, México. Photographs by Photographic Services.

PLATE VI

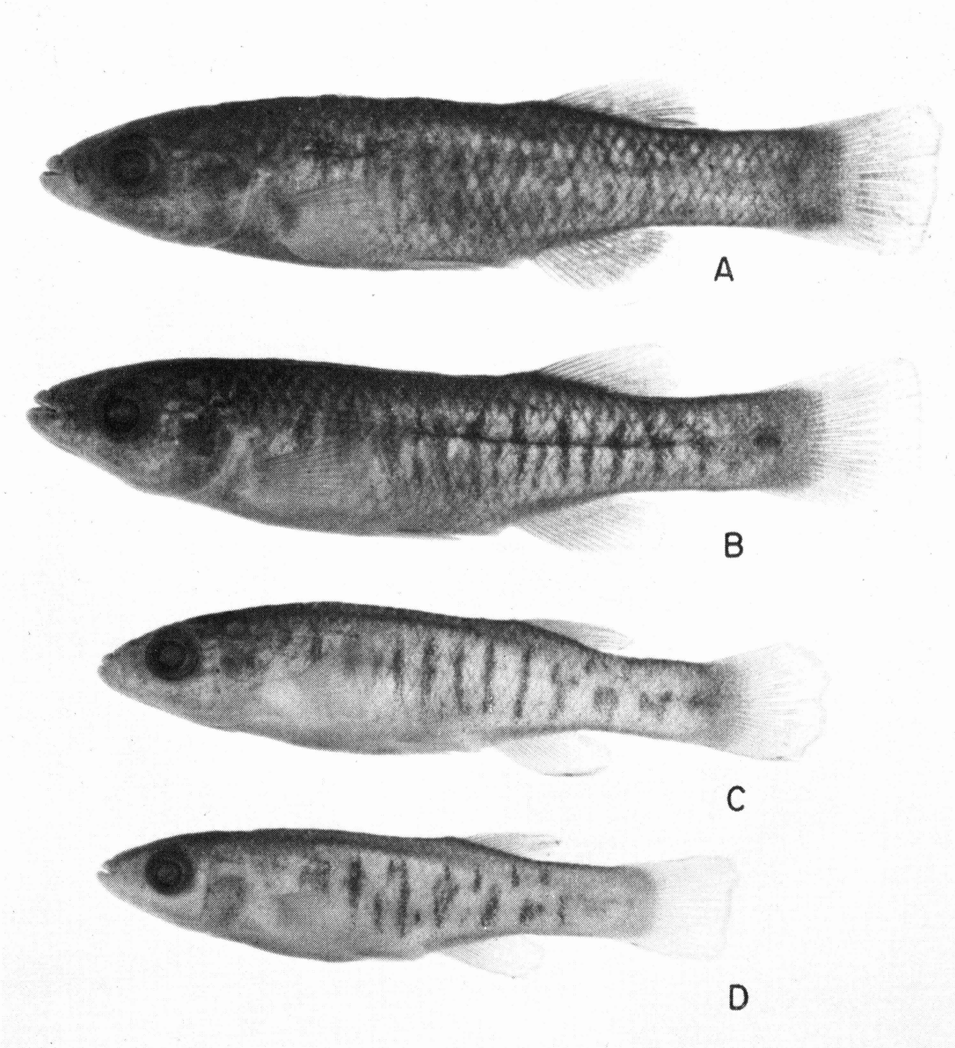


PLATE VII

Profundulus labialis

Adults from the Atlantic drainage of Guatemala (A–B) and México (C–E). For localities, see Maps 1–2.

A. Topotypic male, 49 mm., USNM 134632, Río San Jerónimo at San Jerónimo.

B. Female, 50 mm., UMMZ 166698, Río Carchelá 18 miles by road N of Salamá.

C. Male, 44.5 mm., UMMZ 167057, Río Chico at Chiapa de Corzo.

D. Male, 41 mm., same data.

E. Male, 39 mm., same data.

Photographs by Photographic Services.

PLATE VII

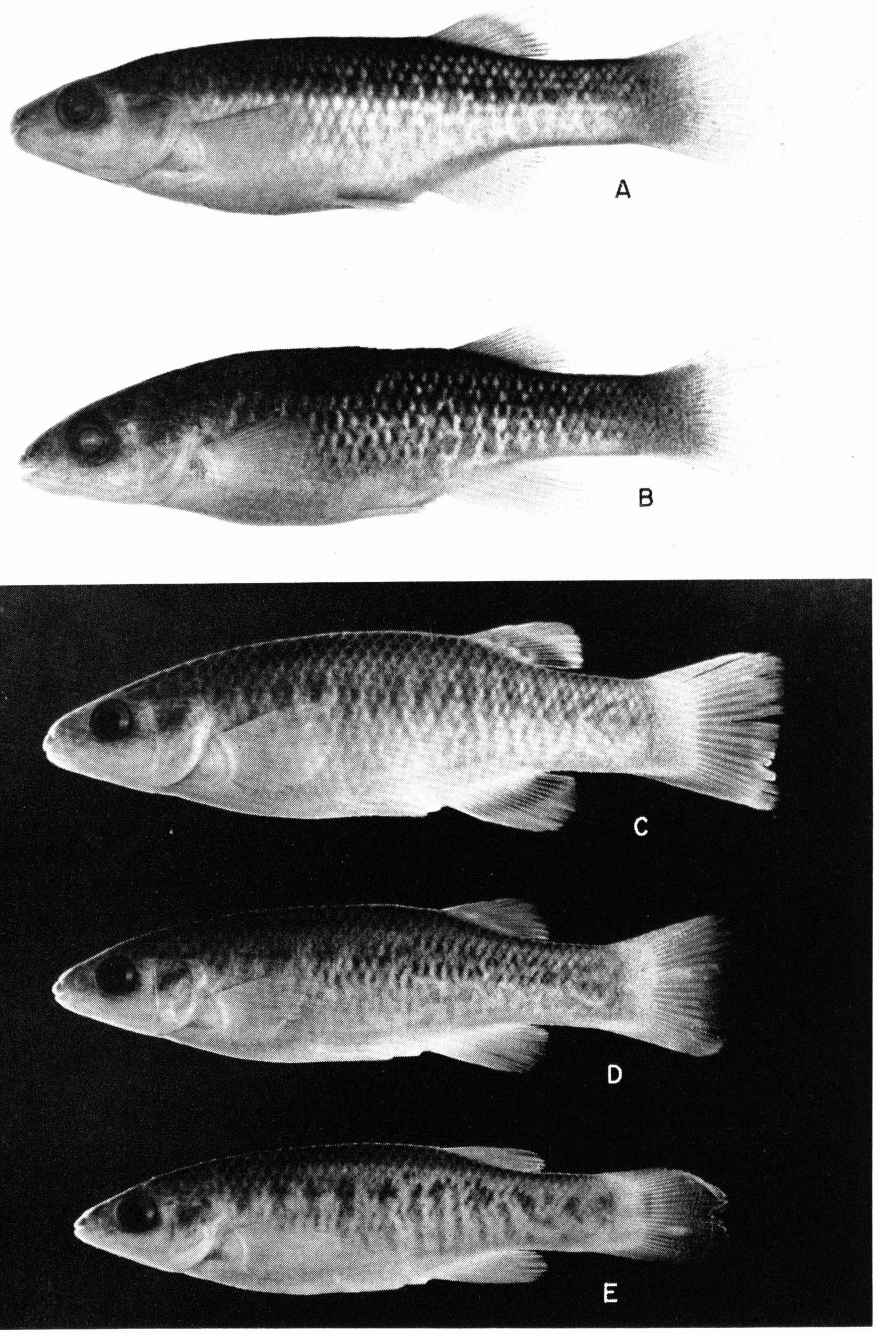


PLATE VIII

Profundulus labialis

Adult and immatures from the Atlantic drainage of Guatemala. For localities, see Maps 2–3.

A. Female, 65 mm., UMMZ 105456, Pansamalá (Polochic Basin). Photograph by Clarence Flaten.

B. Immature female, 33 mm., USNM 144390, Río Negro 6 miles WSW of Quiché.

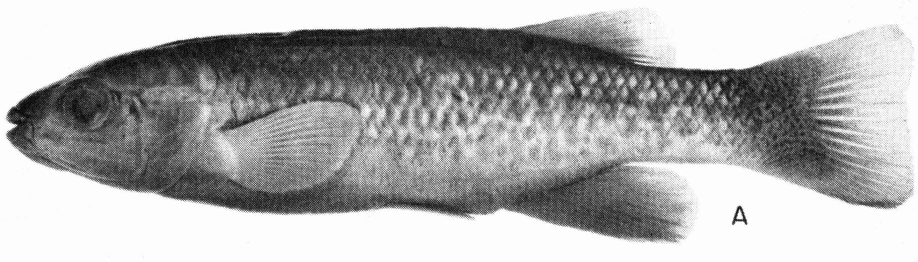
C. Immature, 32 mm., same data.

D. Immature, 25 mm., same data.

E. Immature, 23 mm., same data.

Photographs (B–E) by Photographic Services.

PLATE VIII



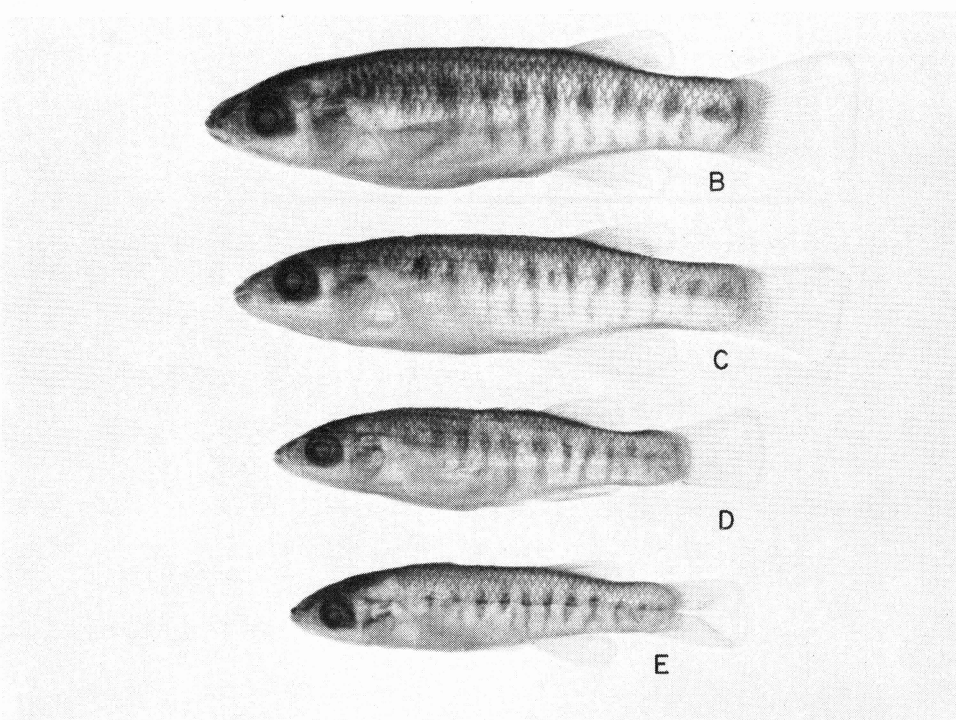


PLATE IX

Profundulus candalarius

Above: Male, 49 mm. UMMZ 166670, Río Grande de Comitán at Yocnajab, Chiapas, México (Map 1).

Below: Female, 50 mm., UMMZ 166673, La Ciénega, 1 km. NE of Comitán, Chiapas.

Photographs by Photographic Services.

PLATE IX

(CONTINUED FROM INSIDE FRONT COVER)

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