

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 127

Studies of Cyprinodont Fishes. XXII.
Variation in *Lucania parva*, Its
Establishment in Western United
States, and Description of a New
Species from an Interior Basin in
Coahuila, México

BY

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AND

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ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
SEPTEMBER 30, 1965

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CONTENTS

INTRODUCTION	5
ACKNOWLEDGMENTS	6
GENERIC LIMITS OF <i>Lucania</i> AND SYNONYMY OF SPECIES	7
VARIATION OF <i>Lucania parva</i> IN ITS NATIVE RANGE	12
Variation in Numbers of Fin Rays, Scales, Vertebrae, and Gill Rakers	13
Variation in Cephalic-Pore System	24
Morphometric Variation	33
Discussion of Local Variants	35
ESTABLISHMENT OF <i>Lucania parva</i> IN WESTERN UNITED STATES	43
San Francisco Bay, California	44
Yaquina Bay, Oregon	45
Timpic Springs, Utah	45
Blue Lake, Utah	47
Irvine Lake, Southern California	47
Source of <i>Lucania</i> Populations in Utah and Southern California	48
Source of <i>Lucania</i> Populations in San Francisco and Yaquina Bays	49
Meristic and Morphometric Evidence on the Origin of the Western Populations	52
<i>Lucania interioris</i> , NEW SPECIES	55
Relationships	55
Comparison with <i>Lucania parva</i>	56
Description	58
Breeding Behavior	59
Types	60
Habitat and Associated Fishes	61
Distributional Relations	62
Differentiation within <i>Lucania interioris</i>	65
SUMMARY AND GENERAL CONCLUSIONS	66
LITERATURE CITED	99

ILLUSTRATIONS

PLATES

(Plates I-III follow page 105)

I. Diversity of *Lucania parva* in Florida

II. Comparison between samples of *Lucania parva*
from Pecos River and Timpie Springs

III. Habitat of *Lucania parva*

FIGURES IN TEXT

FIGURE	PAGE
1. Distribution of <i>Lucania parva</i> and <i>L. interioris</i>	8
2. Variation in numbers of dorsal and anal rays	15
3. Correlation between numbers of dorsal and anal rays	17
4. Variation in numbers of caudal and pectoral rays	18
5. Variation in numbers of scales around body and gill rakers	21
6. Variation in numbers of vertebrae	23
7. Variation in numbers of cephalic sensory pores	27
8. Holotype of <i>Lucania interioris</i>	57

INTRODUCTION¹

THIS paper has stemmed from the unexpected discovery by the senior author in 1939 of a new species, which, though clearly referable to the essentially marine, eastern North American funduline genus *Lucania*, is confined to the largely isolated interior waters of the Cuatro Ciénegas Basin, Coahuila, México. This discovery led to a study of geographic variation in the well-known rainwater fish, *Lucania parva* (Girard), which was found to range along the continental coast from the south side of Cape Cod, southern New England, to the lower part of the Río Pánuco system in the vicinity of Tampico, México (Fig. 1). These studies were an integral part of the now long-deferred revision of the freshwater fish fauna of northeastern México, which was undertaken in 1930 by the senior author and the late Myron Gordon. In that study, the Cuatro Ciénegas Basin appeared, on the basis of collections by E. G. Marsh, Jr., in 1939, to be the site of a high incidence of endemism. Three of the other endemics, two confined to the basin and the other also occurring more widely in the Río Salado system of the Río Grande drainage, have recently been described by Minckley (1962) and by Miller and Minckley (1963). Other endemic fishes of the basin are under study. One of the most notable of the local endemics (autochthonous or relict), is a largely aquatic and probably primitive box turtle, *Terrapene coahuila* Schmidt and Owens (1944:101-03; see also Williams, 1960, and Webb, Minckley, and Craddock, 1963). Several other autochthonous and relict reptiles and amphibians have been discovered in the basin (Legler, 1960; Milstead, 1960; Webb and Legler, 1960; Williams, Smith, and Chrapliwy, 1960; Webb, 1961:292; 1962; Duellman and Zweifel, 1962). The small aquatic gastropods of the basin also exhibit spectacular endemism (Dwight W. Taylor, personal communication).

Very recently the research on *Lucania* has been further expanded as a result of the sudden appearance, for no immediately apparent reason, of *L. parva* in five places in the western United States: about San Francisco Bay in California and about Yaquina Bay in Oregon; in two completely isolated spring-fed waters, Timpie Springs and Blue Lake, in the basin of Pluvial Lake Bonneville in Utah; and in Irvine Lake, a reservoir in southern California. The analysis of the geographic variation of *Lucania parva* in its native range was then expanded, in an effort to indicate the source of the stocks that have somehow been introduced into the West.

¹ Contribution from the Scripps Institution of Oceanography, University of California, San Diego, and from The University of Michigan Museum of Zoology. Cost of publication has been subsidized by the authors, through National Science Foundation grants and a personal contribution.

ACKNOWLEDGMENTS

We have received considerable aid in the long-continued preparation of this paper. First we pay tribute to the late Myron Gordon, with whom the senior author worked for many years on the fishes of northeastern México. Ernest G. Marsh, Jr., kindly made available his collections of 1939 from Coahuila, including the first material of *Lucania interioris*, which stimulated our further exploration of the Cuatro Ciénegas Basin. W. L. Minckley generously donated to The University of Michigan the specimens of this new species that he and James E. Craddock had collected in 1960, provided a map of this desert basin (modified as an insert in Fig. 1), and supplied critical notes on the life colors of the breeding males. José Lugo, Jr., through his wide knowledge of the hydrology of the Cuatro Ciénegas Basin and through his enthusiastic and efficient guiding, enabled us in 1961 and W. L. Minckley on several other occasions to reach remote water holes where we collected large populations of undescribed fishes, including *L. interioris*.

Critical comparative material of *L. parva* from within its natural range was loaned by Clark Hubbs, Edward C. Raney, and Royal D. Suttkus. As is specified elsewhere in this report, data and/or specimens bearing on the establishment of *L. parva* in western United States have been furnished by Jay D. Andrews, Carl E. Bond, W. P. Breese, R. E. Dimick, Willis A. Evans, W. I. Follett, Donald C. Hales, E. W. Kirschbaum, William A. Newman, Keith W. Radford, James A. St. Amant, Leo Shapovalov, Phillip R. Sloan, John A. Thompson, and Howard O. Wright. Neal R. Foster (personal communication) provided valuable observations on the life colors and behavior of *L. parva*, *L. goodei* Jordan, and *L. interioris*, as did Clark Hubbs for *L. parva*. Effective help in field work and in the preparation of this report was given by our wives, Laura Clark Hubbs and Frances Hubbs Miller. The illustration of the holotype of *L. interioris* was drawn by Suzanne Runyan, former staff artist of The University of Michigan Museum of Zoology. James R. Moriarty, of Scripps Institution of Oceanography, took special pains in preparing the map (Fig. 1) and the graphs.

Financial support for this research has been provided by the National Science Foundation, through grants to the authors (G-15928 to Hubbs and G-24129 to Miller). Participation by Miller in the Cuatro Ciénegas field work of 1961 was made possible by a research grant (Proj. 1227) from the Horace H. Rackham School of Graduate Studies of The University of Michigan.

For loan or records of critical material we are deeply indebted to the directors and curators of several museums, as follows (with abbreviations used in recording the specimens):

ASU, Arizona State University; CAS, California Academy of Sciences; CU, Cornell University; INIBP, Instituto Nacional de Investigaciones Biológicas Pesqueras (México); OSU, Oregon State University; SIO, Scripps Institution of Oceanography; TU, Tulane University; UK, University of Kansas Museum of Natural History; UMinn, University of Minnesota; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum; UT, University of Texas.

GENERIC LIMITS OF *LUCANIA* AND SYNONYMY OF SPECIES

Current reconsideration of generic limits in the funduline Cyprinodontidae, marked by the re-reference of *Chriopeops goodei* to *Lucania* (Briggs, 1958:265; Bailey, *et al.*, 1960:22), has prompted an analysis of the more basic characters of that species, as well as those of *Lucania parva* (including its synonym *Lucania venusta*), the Cuatro Ciénegas endemic (*Lucania interioris*), and other species that have been referred to *Lucania*.

Lucania parva was originally described as *Cyprinodon parvus* by Baird (1855:345 = p. 31 of separate). There is no doubt as to the pertinence of the specific name, but a change in authorship now seems called for. Jordan and Gilbert (1883:343, 893) referred the species to "B. & G." assertedly on information from Tarleton H. Bean. Jordan and Evermann (1896:665-66) and subsequent authors have written the name *Lucania parva* (Baird and Girard). But the species, though the name was given as "*Cyprinodon parvus*, B. & G.," should be accredited to Baird alone. A scientific name, according to Article 50 of the new International Code of Zoological Nomenclature, must be accredited to the author of the original publication, in this case Baird, because it is not clear "from the contents of the publication" that Baird and Girard were "alone responsible both for the name and the conditions that make it available." The only reference to Girard's participation in the publication was Baird's remark (p. 318): "For important assistance in determining the species I am under many obligations to Mr. Girard." (The same change in authorship applies to the generic name *Eucinostomus* and to the species name *E. argenteus*.)

As will be obvious from the analysis given below of geographic variation in *Lucania parva*, *Limia venusta* Girard (1859a:71, pl. 39, figs. 20-23), the type species of *Lucania* Girard (1859b:118), is clearly a synonym of *L. parva*. The synonymy of *L. parva* and the status of other species that have been referred to *Lucania* was discussed by Myers (1925:370) and by Hubbs (1926:5-6). The following analysis of regional variation in *Lucania* (*sensu stricto*) leaves no vestige of a reason for recognizing two species (*L. parva* and *L. venusta*). In separating these "species" Jordan and Evermann (1896:663-66) relied largely on the slender body of *venusta*

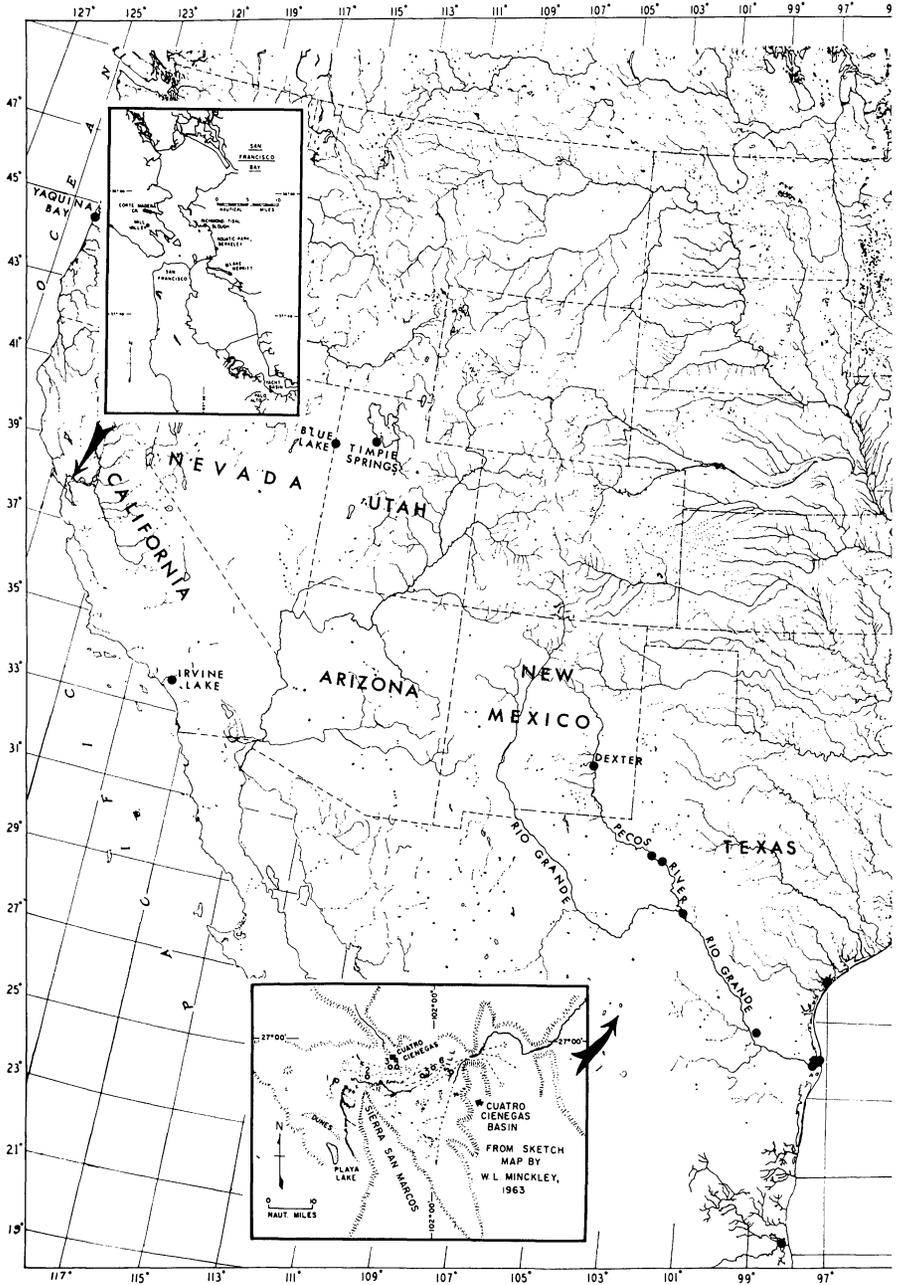
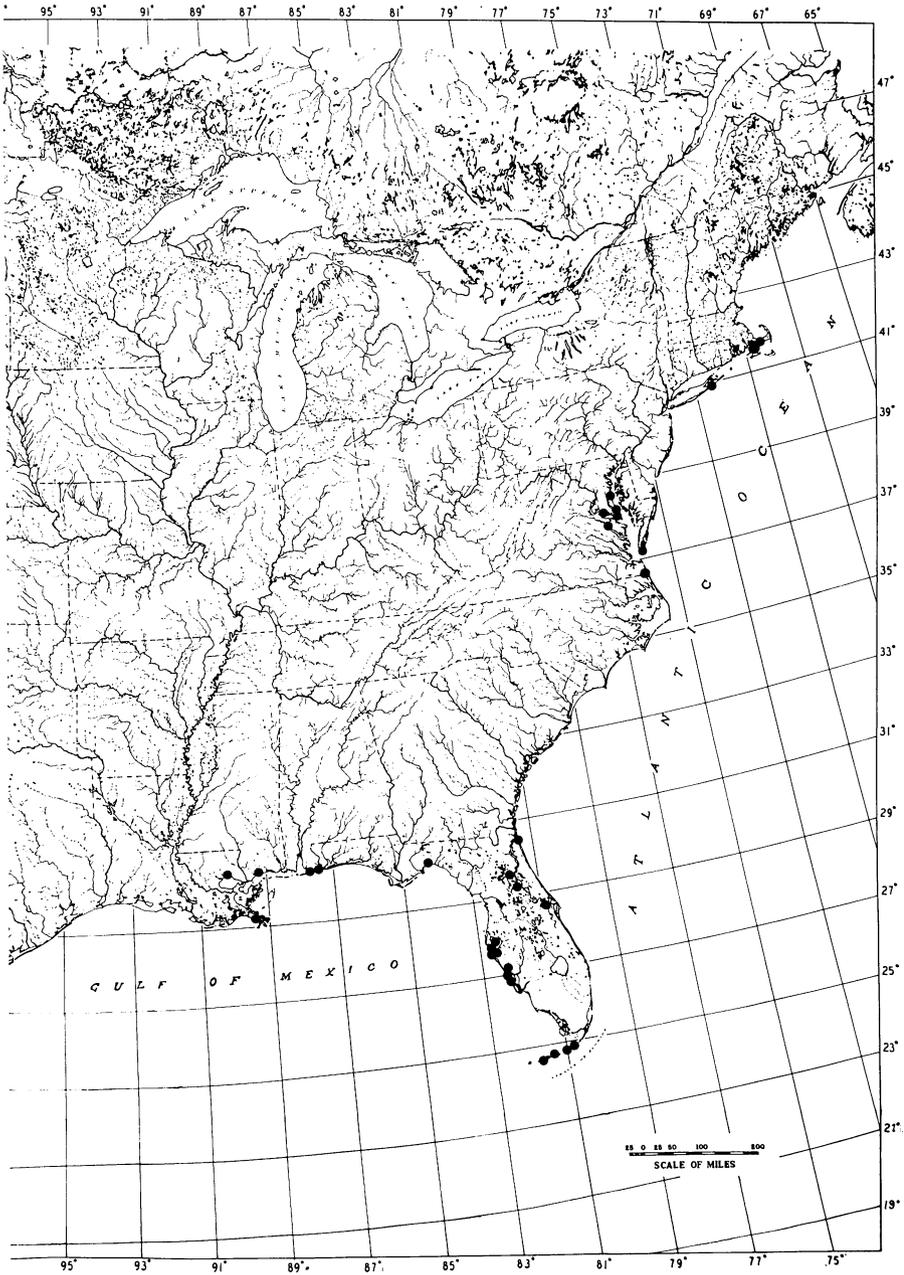


FIG. 1. Distribution of *Lucania parva*, where native in the east and introduced in the west, and of *L. interioris* (in one interior basin in México). Record stations for *L. parva* along the Atlantic Coast and in Pecos River are plotted only for the collections uti-



lized in the study. The inserts, of the Cuatro Ciénegas Basin and of San Francisco Bay, show all known occurrences of *Lucania* in these areas.

and referred to *parva* deep-bodied specimens of the otherwise trenchantly different races of southern Massachusetts and Key West (they, following Jordan, 1884, based their description of *parva* on material from Key West). Body depth (Table 22) varies too much and too irregularly to justify even subspecific separation. Differences in number of dorsal and anal rays were inconsistently indicated by Jordan and Evermann and are definitely not of specific or subspecific value (Tables 2 and 4, Fig. 2). Some recent authors, on the now abandoned decision of the senior author, have recognized a Gulf subspecies, as *L. p. venusta*; one such usage was that of Knapp (1953:88), who wrongly restricted its range to coastal waters and illustrated it with a copy of Jordan and Evermann's figure (1900:3256, pl. 109, fig. 292) of a specimen from New Jersey, representing the northern type which would be typical of *L. p. parva*, if subspecies were to be separated.

Lucania affinis Girard (1859b:118-19), from Matamoras, Tamaulipas, México, near the mouth of Río Grande, has long and properly been treated as a synonym of *L. venusta*, and hence also of *L. parva*.

An examination of the literature disclosed the probability that another nominal species, *Limia poecilioides* Girard (1859a:70-71, pl. 114 of volume = 38 of separate, figs. 8-14) pertains in part to *Lucania parva*. The two type specimens, a male and a female, were collected in 1851 by John H. Clark, on the party of Col. J. D. Graham, during the United States and Mexican Boundary Survey, at Indianola, on the coast of Texas [on Matagorda Bay, in Calhoun County]. They were so recorded in the Boundary Survey report and were so entered in the Smithsonian catalog on March 29, 1858, but no trace can be found of either specimen, in either the type or non-type series in the United States National Museum. The figures of the male (8-11) show that it was clearly a specimen of *Poecilia latipinna* (Lesueur), but the figures (12-14) of the female, we believe, were based on a specimen of *L. parva*. The characters pertinent to this conclusion are: the very short dorsal fin (with count given as 8 instead of 13 for the male); the anal larger than the dorsal (with count given as 12 instead of the low 6 count given for the modified anal fin or gonopodium of the male); the almost uniform color, as also described, with cross hatching on the scale pockets rather than being prominently marked with a black spot on each scale; the more compressed body; the rather rhombic general form, with relatively slender caudal peduncle; and the rounded rather than truncate muzzle in dorsal view, with narrower mouth. A copy of the Boundary Survey report in the National Museum having the lithographed plates colored shows colors much like *L. parva*: olive above and blue-gray on the lower sides, becoming yellow-gray on the ventral surface; the fins slightly yellow; considerable gilt on the opercle, and stronger gilt on the posterior part of the cheek. It seems virtually certain that *Limia poecilioides* as

described and figured was a complex. As first revisers we synonymize *Limia poecilioides* Girard with *Poecilia latipinna*.

The four names applied to *Lucania parva*, as just noted, were all proposed in the 1850's and were referred to three genera (*Cyprinodon*, *Limia*, and *Lucania*). Three of the nominal species were described by Girard, who participated in the identification of the fourth. Such taxonomic variance was almost a habit of this author.

As noted in the description of the new species, *Lucania interioris* is referable without question to *Lucania*.

The species that was originally described as *Lucania browni* by Jordan and Richardson (1907), on the basis of specimens from a hot spring in the Laguna Salada Basin of Baja California (the site of Pluvial Lake Pattie of Hubbs and Miller, 1948:112-13), has for years been known, following a re-examination of the type (Hubbs, 1926:6), as a synonym of *Cyprinodon macularius* Baird and Girard.

Another species that has been referred to *Lucania*, for example by Jordan and Evermann (1896:663), namely *Leptolucania ommata* (Jordan), differs in fundamental characters sharply from the species we admit in *Lucania* (Table 1), and, we feel, represents a separate phyletic line entirely worthy of recognition at the generic level.

The species originally described by Jordan as *Lucania goodei*, although for a time allocated to *Fundulus* and for some decades generally referred to a monotypic genus *Chriopeops*, now appears to be more satisfactorily reclassified as a subgenus under *Lucania*. *Chriopeops* has been distinguished primarily on the basis of dentition; the teeth of the jaws are definitely biserial in *goodei*, with those of the inner row weak, and are reputedly uniserial in *parva*, but the single row in *parva* is often more or less irregular, and in some specimens a few teeth, though strong like those of the main row, are interpretable as forming a second row. This supposed generic distinction is therefore weakened. In many other characters, including those that distinguish *Leptolucania*, the species *goodei* and *parva* are much alike (Table 1). Certainly there appears to be little if any merit in the suggestion by Jordan and Evermann (1898:2831) that *goodei* should be referred to *Fundulus*, while *parva* is retained in *Lucania*. Furthermore, *L. goodei* and *L. parva* occasionally hybridize in nature (Hubbs, Walker, and Johnson, 1943:8-15, pls. 4-6), whereas neither has been found to hybridize in nature with any other species (Hubbs, 1955:12). This occasional hybridization may be taken as an indication of consanguinity.

The genus *Lucania*, as we now conceive it, therefore comprises three species, *L. parva*, *L. interioris*, and *L. goodei*, and ranges along the Atlantic coast of eastern North America from southern New England to northeastern México. There are no indications of its occurrence in the Bahamas,

Bermuda, or the Antilles, though *Fundulus cubensis* Eigenmann was referred to *Chriopeops* by Myers (1925:370). That Cuban species is currently placed in a monotypic genus, *Cubanichthys* Hubbs (1926:4). *Cubanichthys cubensis* and the Jamaican *Chriopeoides pengelleyi* Fowler (1939:4-5, figs. 3-4) may be closely related to *Lucania*.

The geographic limits of *Lucania* are therefore continental, and are essentially those of *L. parva*. *L. interioris* occupies a single interior basin in northeastern México, outside of the range of *L. parva*, and *Lucania goodei* is largely confined to the fresh waters of the Florida Peninsula (Kilby and Caldwell, 1955:204; Briggs, 1958:265), but penetrates into brackish water (Hubbs, Walker, and Johnson, 1943:8; Kilby, 1955:203; Tabb and Manning, 1961:614). From the south side of Cape Cod through Georgia *Lucania parva* occurs chiefly in protected salt water and in brackish coastal waters, but in Florida it ranges from marine localities on keys and in bays through freshwater habitats, some considerably removed from the coast; in at least some coastal marshes it lives chiefly in waters of low salinity (Kilby, 1955:202; Tabb and Manning, 1961:615). West of Florida it is again chiefly coastal, but at different localities it predominates in waters of low, medium, or even high salinity (Simpson and Gunter, 1956:122; Renfro, 1960:87). It penetrates for a considerable distance up the Río Grande (Robinson, 1959) and is represented by an abundant population in the rather highly mineralized lower portion of the Pecos River (Clark Hubbs, 1957:99). Near the coast it presumably extends from the Río Grande to known occurrences in the lower reaches of the Río Pánuco system near Tampico, Tamaulipas, México (Darnell, 1962:329, and personal observation).

VARIATION IN *LUCANIA PARVA* IN ITS NATIVE RANGE

In view of its very wide range in latitude and in habitat, it is not surprising to find that *Lucania parva* is a highly variable species (Figs. 2, 4-7, Pls. I-II, and Tables 2-26). Though large differences distinguish many populations, we find the variations too complicated to warrant, at least at the present time, any division of the taxon into subspecies. In some characters there is a tendency toward a north-south cline, but differentiation seems to be accentuated in Florida (see discussions below), and the most interior population, that of Pecos River, as is also indicated below, somewhat approaches the southern New England populations in certain characters (suggesting the slight possibility that the Pecos form may be a relict, dating from a Pleistocene glacial time of southward dispersal).

Because many of the differences between populations involve body form and other characters known to be directly affected by environmental factors, and because even the meristic differences may have at least partly

an environmental basis, it seems obvious that the significance of the local variations cannot be interpreted with full confidence until they have been subjected to extensive experimental tests, either under controlled laboratory conditions or through transference experiments in nature. To a degree, inferences of probable significance in this connection can be, and to some extent have been, made through the critical analysis of changed characters in new environments into which the species has by chance been introduced, almost surely from regions where the characters have been determined; and through the analysis of the characters of natural populations subject to a variety of known environmental conditions. The complex situation in Florida (p. 38) seems particularly inviting for such experiments. We commend the problem to anyone in a position to attack it.

The apparently reduced number of dorsal and anal rays in the localities where the species has been introduced in the western United States, as discussed later (p. 53), appears to indicate a direct phenotypic response. The apparent trend toward fewer rays in warmer water calls to mind the evidence that such a correlation appears to hold for the dorsal fin of certain poeciliids, whether on a phenotypic or genotypic basis; experiments by Schmidt (1919*a, b*) showed a phenotypic response in this direction for the dorsal rays of *Lebistes*, although rearing experiments by Hubbs and Hubbs (unpublished) showed that the often-observed positive correlation in nature between environmental temperature and dorsal-ray number in other poeciliids is genetically determined, for the varying numbers of rays in different races are retained with high fidelity when all are reared under essentially identical aquarium conditions.

The marked geographical variation in number of sensory pores on the head (Tables 16–19, Fig. 7) involves structures that are completely formed and fixed relatively late in the development of the fish, and hence may be subject to modification not only by genetic factors but also by such environmental factors as modify rates of growth and differentiation. In aquarium- and pond-reared cyprinodonts of other genera we have observed delayed or incomplete formation of these pores.

Before proceeding to a more general geographic consideration of differentiation within *Lucania parva*, we discuss the variational data for individual characters.

VARIATION IN NUMBERS OF FIN RAYS, SCALES, VERTEBRAE, AND GILL RAKERS

NUMBER OF DORSAL RAYS (Tables 2 and 3, Fig. 2).—The dorsal rays were enumerated on the principle of treating as the last ray the two terminal elements that are distinct through their hidden bases. For much of the subadult and adult material the anterior unbranched and the branched

rays were also separately enumerated (Table 3), as recommended by Hubbs and Lagler (1958:21).

The number of dorsal rays exhibits wide variation, from 9 to 14. Throughout the range of the species by far the most frequent number is 11, though in a few areas, as the bays and keys of western Florida (but not about the Florida Keys nor in Pensacola Bay), counts of 10 are about as frequent as those of 11. In collections from more interior localities in Florida the average number is increased, and 12-rayed fins are nearly or quite as common as 11-rayed fins, or, locally, as in Juniper Springs Creek, even commoner. There seems to be a cline in Florida, with the number lowest on the west coast bays and keys and highest in the interior. There is a slight negative skewness in the number of dorsal rays, largely because extreme variants appear to be on the high side.

In this species the number of unbranched dorsal rays in the subadults and adults (selected for size to avoid most of the uncertainty owing to late branching in development) is so predominantly 2 throughout the range that we present only the grand totals (Table 3) for unbranched and branched rays. The highest average number is for the mouth of the Río Grande, where the frequencies of the 26 counts are 2 in 13 specimens, 3 in 12, and 4 in one. The number of branched rays reflects little more than the fluctuation in total-ray count; the modal number is usually 9, but drops to 8 near the mouth of the Río Grande and rises to 10 in Juniper Springs Creek, Florida; intermediate conditions also reflect fluctuations in the total count.

NUMBER OF ANAL RAYS (Tables 4 and 5, Fig. 2).—The anal rays were enumerated in the same way as the dorsal rays, and again the unbranched and branched rays were separately counted in much of the material.

The number of anal rays shows the same range of variation (6) as the dorsal rays; the extreme counts are 8 and 13 rather than 9 and 14, and the modal number is usually one or two fewer (usually the dorsal-ray number on the average exceeds the anal-ray number by about 1.5). The grand mean is 9.49 rather than 10.96. The modal number is consistently either 9 or 10, with these numbers about equal at some localities. Deviations from the grand mean rather closely follow those for the dorsal rays. Counts of 9 tend to predominate in the north and in the Florida Keys and on the keys and in the bays of west Florida; along the Gulf coast west of Florida 10 is the predominant number, but this drops to 9 in two of the three collections from the lower Río Grande and in the several series from the Pecos. Hence, the latitudinal cline is slight and very irregular. As for the dorsal rays, the average number of anal rays in Florida exhibits a cline, increasing from marine to freshwater habitats. Negative skewness is even

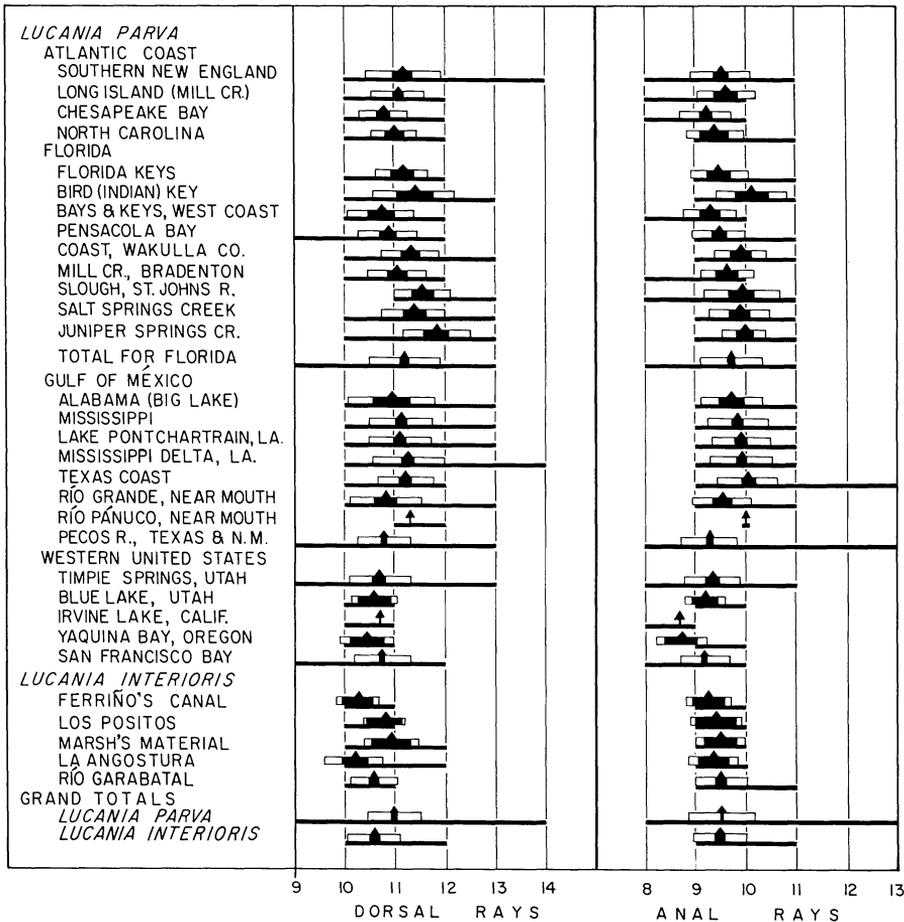


FIG. 2. Geographical variation of *Lucania parva* and *L. interioris* in numbers of dorsal and anal rays.

The method of graphical analysis is that of Hubbs and Hubbs (1953), portraying the range, one standard error on either side of the mean (indicative of differentiation), two standard errors on either side of the mean (indicative of reliability), and the mean. Further tests of differentiation and of statistical reliability are explained in the paper cited.

more marked than for the dorsal fin, because in occasional specimens the number is exceptionally high.

Regional fluctuations also characterize the number of unbranched and branched anal rays (Table 5). Without any apparent pattern the unbranched rays are predominantly either 1 (as in Chesapeake Bay and in Lake Pontchartrain), or 2 (as on the Texas coast), or about equally 1 or 2 (as in

the Long Island and in most Florida samples). The number of branched rays may vary less with locality in some general regions, as in Florida, or more, as in the tabulated sequence from Lake Pontchartrain to the Pecos River. For the anal fin the correspondence between fluctuations in branched-ray and total-ray counts is less marked than for the dorsal fin.

CORRELATION BETWEEN NUMBER OF DORSAL AND ANAL RAYS (Table 6, Fig. 3).—Since the average numbers of rays in each fin fluctuate geographically and since there is a rather uniform difference between the numbers of rays in the two fins, these numbers are positively correlated when the entire species is considered. This is shown by graphing the associated averages (Fig. 3). In agreement with the general law that counts in dorsoventrally or bilaterally opposed series are positively correlated (Hubbs and Hubbs, 1954:192) the numbers of rays in the more or less opposed dorsal and anal fins, in both species, show positive correlation in any one region, as indicated in Table 6 for three single collections and for two integral groups of collections; the other, smaller series also showed such correlation. Two sets, for Timpie Springs and the San Francisco Bay region, may each well comprise progeny from a single introduction, or at least from the same local population, and hence are probably very uniform genetically. That these two show approximately the same degree of correlation between dorsal and anal rays as do collections from throughout the range of the species suggests that the correlation involves more than the mere mixing of stocks that are low or high in ray number in both fins. In other words, the correlation is presumably individual as well as racial.

NUMBER OF CAUDAL RAYS (Table 7, Fig. 4).—The number of caudal rays, as we have been counting them in cyprinodont fishes, is the number of branched rays plus 2. This is the standard method for typically forked caudal fins, in which the rays ordinarily counted are the principal rays, including one strong marginal ray above and one below. In *Lucania*, as in other cyprinodonts, the only test used is whether the ray is branched—a determination that may require rather high magnification under strong light. Although the complete branching pattern is usually established in subadults, and the caudal rays were not counted in young specimens, some reserve is called for in interpreting differences in caudal-ray numbers; occasionally an additional ray or two apparently branches at its tip in a large adult.

The local differences in average and modal numbers of caudal rays are almost surely locality-dependent, and are probably race-dependent as well. The range is high (12 to 18), as it often is in cyprinodonts (Hubbs, 1936: 212-25; Miller, 1948:98) and other fishes with a rounded caudal, as contrasted with the usual almost invariable number, within whole families, for fishes with a forked caudal fin. The mode varies with locality, with no

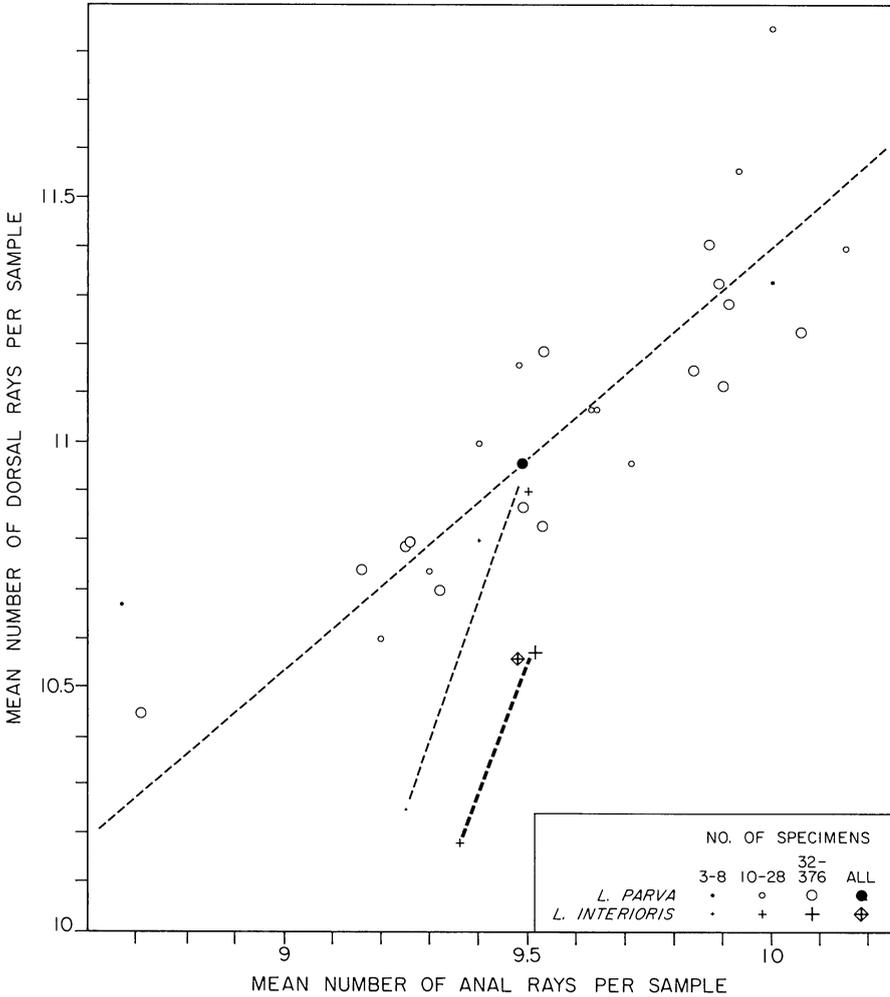


FIG. 3. Correlation between numbers of dorsal and anal rays in both species of *Lucania*, throughout their respective ranges.

The regression lines were fitted by eye. The two lines for *L. interioris* (both very steep) represent what may be two subpopulations (p. 65).

clear-cut cline, from 14 to 16, and the means vary correspondingly. In the diverse series from Florida there is a suggestion of a positive cline from the Florida Keys to the freshwater stocks.

NUMBER OF PECTORAL RAYS (Table 8, Fig. 4).—In counting the number of pectoral rays, separately for each fin, the uppermost short ray was included, and care was taken, with magnification, light, and manipulation, to include even the most minute lowermost ray. Separation of unbranched

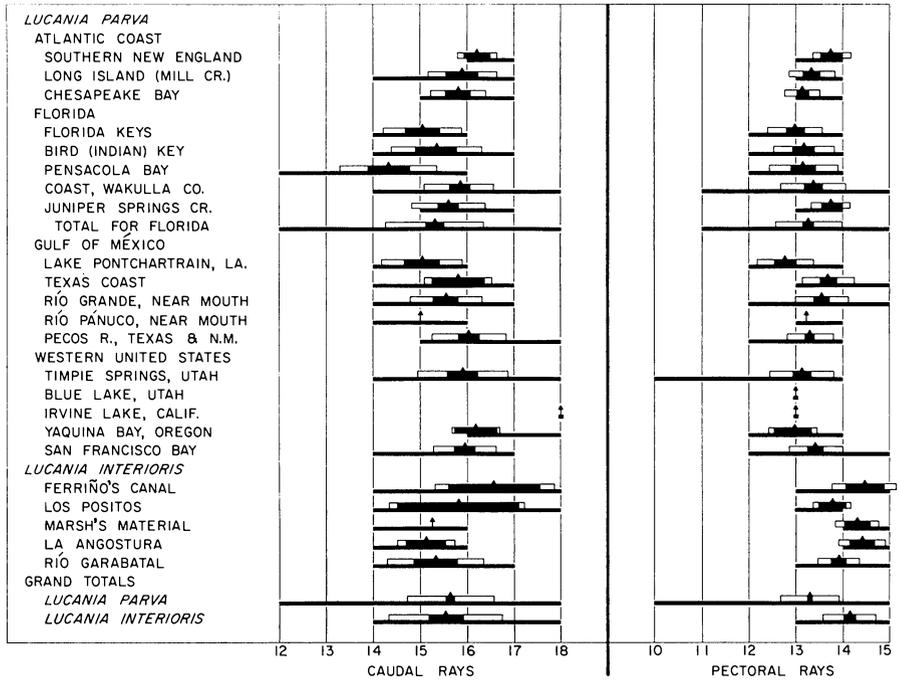


FIG. 4. Geographical variation of *Lucania parva* and *L. interioris* in numbers of caudal and pectoral rays. For method of analysis see Figure 2.

and branched rays was neither practicable nor significant; almost invariably the second ray is upper-marginal and unbranched, and the third and following are branched, whereas in the lower part of the fin the branching gradually fades out, so that the distinction becomes not only difficult but also tenuous in the almost microscopic rays, which end in diffuse tissue, including ceratotrichia.

The number of pectoral rays varies from 12 to 15, with one count of 10 and one of 11, each in an apparently uninjured fin. In this species the modal number is consistently either 13 or 14, or 13 and 14 occur in about equal frequency. The mode is most frequently 13, but is indicated by the counts to be 14 in southern Massachusetts, in Juniper Springs Creek, Florida, and along the Texas coast. The only suggestion of a cline is toward a slightly higher average number from the Florida bays and keys to the freshwater, interior habitats.

ANALYSIS OF BILATERAL ASYMMETRY IN THE NUMBER OF PECTORAL RAYS (Table 9).—As is usual in fishes (Hubbs and Hubbs, 1945:264–75), there is some asymmetry between the numbers of pectoral rays in the left and right

fins of *Lucania*, superimposed on the expected positive correlation. In approximately one-fourth of the specimens the number is different on the two sides. There may be a slight tendency for the higher number on the right side, though the departure from equality yields a low chi-square value (1.76 for *L. parva*, 0.69 for *L. interioris*, and 2.37 for the two species combined). Since there is no indication of geographic variation in the extent or direction of asymmetry, the data, which stem from all parts of the known range of the species, are not detailed by locality in Table 9.

NUMBER OF PELVIC RAYS (Table 10).—No complications arose in counting the pelvic rays, except that, very rarely, adjacent rays are somewhat fused. In one specimen from the San Francisco Bay region the left pelvic fin is paired, with 5 rays in each of the similar, slightly reduced fins, which lie in contact; its single right pelvic is normal in size and in having 6 rays. Occasional specimens of *L. parva* have 5 or 7 rays in one pelvic, which is usually but not invariably matched by a fin on the opposite side with 6 rays. One specimen of *L. parva* has 4 rays in one pelvic fin, but none, among the many examined, lacks a pelvic fin, though two of *L. interioris* lack the fin on one side, with no indication of injury. Since within either species there appear to be no significant clines nor local variations, only the summary data are presented in Table 10.

NUMBER OF LATERAL SCALE ROWS (Table 11).—The oblique (downward and backward) scale rows were counted as follows: starting with the first oblique row entirely behind upper end of gill opening, excluding scales essentially on the pectoral girdle; continuing backward essentially along axis of body; ending with the scale the exposed surface of which is largely in front of the base of the median caudal rays (see Miller, 1948:9, fig. 1). The enumeration is somewhat tricky, but we were able, using the criteria just stated, to repeat the same count.

The number of rows varies through 7 numbers, from 23 to 29. The modal number is usually 27. The greatest deviation is exhibited by the race of the Florida Keys, where, in correlation with the reduced number of vertebrae, the scale rows are correspondingly few. In this character, as in others, there appears to be a cline in Florida, toward a higher number in the more interior, freshwater habitats; the modal extremes are striking, from 25 to 28.

NUMBER OF SCALES BETWEEN ORIGINS OF DORSAL AND ANAL FINS (Table 12).—This count was made as follows: the count starts at the extreme front of the anal fin, where there usually is a scale in line with others, usually but not always of much reduced size, along the extreme base of the fin (this first scale of the count is sometimes as large as the scales above it, but occasionally is smaller than those along the fin base). The count continues upward and forward, stepping back one oblique row, to front of dorsal

fin. An extra row is included if small scales are inserted between the dorsalmost row of scales, if of normal size, and the front part of fin, even though one of these interpolated little scales does not precisely intervene at the origin of the fin; but this extra row is disregarded if it does not extend approximately to the front of the fin. Some difficulty was experienced in duplicating counts until these criteria were established; recounts were made when seemingly needed.

The variation is limited to four counts (8 to 11, but with only one count of 11). There seems to be a trend toward a reduced number in the south, which trend is not closely correlated with the variations in number of vertebrae (see below). The most frequent number in the far north is 10; the lowest average is in the slender-bodied fish of the Pecos River, among which counts of 8 seem to slightly outnumber those of 9, which is the modal number through most of the range. In the Florida Keys, where the vertebrae and lateral scale rows are few, the dorsal-to-anal count is high—but this is in correlation with the very deep body, which is established early in life. In the extreme race of Juniper Springs Creek, Florida, the number is also high (despite the slender body), as is also the number of lateral scale rows and vertebrae.

NUMBER OF SCALES AROUND BODY (Table 13, Fig. 5).—This count was made as follows: starting with the axial row below origin of dorsal, enumerating rows upward around front of dorsal, including as 2 a pair of scales (usually evident) just in front of the dorsal, if definitely in advance of the extreme front of base of first ray, even though each such scale is isolated and is not part of a row (such scales, as counted, vary from 0 to 2); continuing the count of rows on a zig-zag line, moving slightly forward to round front of pelvis (excluding very minute scales occasionally developed at front of each pelvic); then continuing upward and slightly backward to the row just below the axial row, near point of origin of count. These criteria facilitated duplicate counts.

This scale count proved to be particularly significant in characterizing local stocks. The extreme range is from 18 to 25 (with only one count each of 18 and 25), and the modes vary from 20 to 23. In general the counts are high in southern New England, Long Island, and the Chesapeake Bay region. In Florida there seems to be a positive cline from the more marine to the more interior and freshwater habitats, excepting that the race of the Florida Keys, despite its few vertebrae and few lateral scale rows, has a high circumferential count (again in correlation with the early-attained deep body). Along the Gulf of Mexico coast the averages and modes are low, as they also are in the Pecos River system.

NUMBER OF SCALES AROUND CAUDAL PEDUNCLE (Table 14).—This count is usually made rather readily and with assurance, following a zig-zag

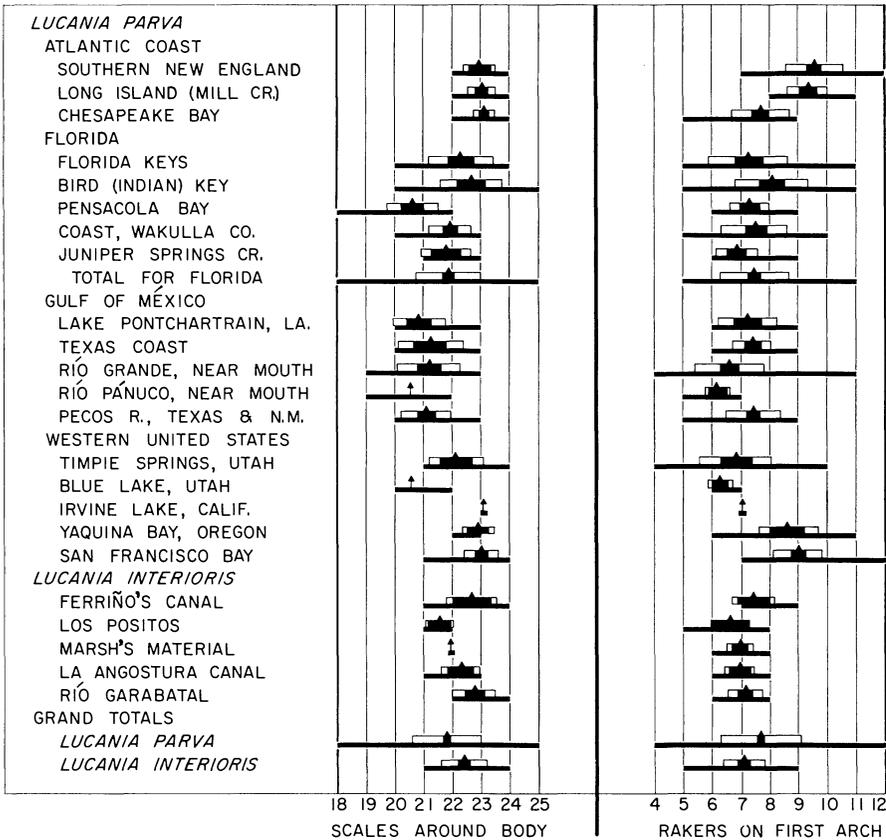


FIG. 5. Geographical variation of *Lucania parva* and *L. interioris* in numbers of scales around body and of gill rakers. For method of analysis see Figure 2.

course around the slenderest part of the peduncle. Occasionally, however, the count carries some uncertainty. This is particularly true of more or less emaciated specimens, such as are frequent in the Pecos River.

Over the whole range of 11 to 16 (with only one count of 11), the maximum number of peduncular scales, oddly, is the most frequent. There is, therefore, a very notable positive skewness. There is also a tendency for even numbers to predominate. Reduction to 12 is common along the Gulf of Mexico coast, but not in the Florida Keys, nor among the interior, freshwater Florida types, despite their slenderness. At some Gulf localities 12 seems to be the modal number, even though there is a secondary mode at 16, so that the frequency distribution is bimodal (a rare phenomenon). These circumstances all militate against applying ordinary statistical calculations.

NUMBER OF VERTEBRAE (Table 15, Fig 6).—The vertebrae were counted on X-ray negatives. Since some difficulty was encountered in distinguishing the precaudal from the caudal vertebrae, only the total count is used. The hypural complex is included as a single unit.

The vertebral numbers vary widely, from 25 to 30, with only five counts of 25 and one of 30. The mode throughout most of the species range is 28. The only observed deviations from this are as follows: In Juniper Springs Creek, Florida, the mode is definitely 29; this count slightly exceeds that of 28 in the series from the Texas coast. The only significant cline seems to be the amazing one in Florida, where the stock of the Florida Keys has the mode at 26, the somewhat less extreme type of the bays and keys along the west coast has the mode at 27, and an extreme stock of the interior, freshwater type (from Juniper Springs Creek) has the mode at 29! The differences here are very sharp: the counts for the Florida Keys and the west coast exhibit a separability at the 85- and 95-per cent level, respectively; between the Florida Keys and the Juniper Springs Creek series, the separability is at the 100-per cent level for each lot. In view of the essential constancy elsewhere, even into México, it seems highly probable that the vertebral variance in Florida is at least in part of genetic basis.

NUMBER OF GILL RAKERS (Table 20, Fig. 5).—The gill rakers are weakly and variably developed in *Lucania*, as in many other cyprinodonts. Consistent counts are obtainable only on the criterion of including all rudiments, which cannot be accurately detected without using adequate magnification and illumination; a fine air jet is a further desideratum. Since the angle of the arch is gentle and the upper arch is rudimentary, and since the development of a raker at or just above the angle (or in both positions) is very inconsistent, the total count only has been recorded. Occasional irregularities in raker structure called for criteria in counting; a two-pronged or even multifid raker, though split nearly to the base, was usually counted as one, but two rakers separated through their bases, though juxtaposed, were counted as two.

As is often true, the number of rakers, despite their degeneracy, provides one of the most distinctive and trustworthy characters. The observed range is very wide, from 4 to 12 (very rarely either 4 or 12), and the modal number varies from 6 to 9. Almost the entire range is shown by single lots, though most of the counts are clustered about the mode. There appears to be a rough cline, from the range of 7 to 12 in southern New England, with subequal modes at 9 and 10 and with 70 per cent at those two numbers, to a range of 4 to 11 in the Río Grande near its mouth, with the mode at 6 and with 74 per cent at 6 and 7. Assuming a break between counts of 8 and 9, the data show the "percentage identifiable" as 84 and 94 for these collections, respectively. This sharpness of separation could serve as a

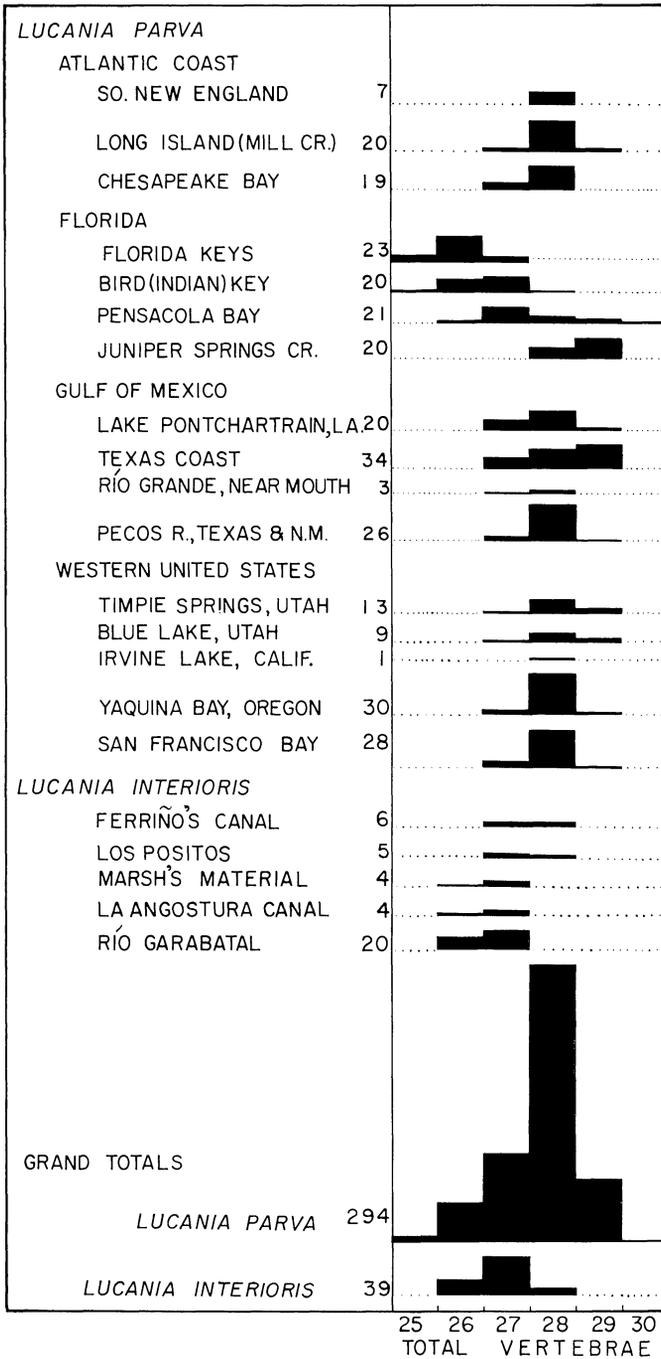


FIG. 6. Geographical variation of *Lucania parva* and *L. interioris* in numbers of vertebrae.

basis for the recognition of subspecies were it not for the intermediate series. In Florida the gill-raker count seems to be reduced also in the interior races, as represented by the series from Juniper Springs Creek. The Pecos race shows the same mode, 7, as the species as a whole, and yields the range from 5 to 9.

VARIATION IN THE CEPHALIC-PORE SYSTEM

The number of pores in the several elements of the sensory-canal system of the head, which follows the pattern of the cyprinodonts outlined by Gosline (1949), provides some of the most useful characters for the distinction of local forms in *Lucania* (Tables 16–19, Fig. 7). The pores in the cyprinodonts comprise four separated groups: preopercular, supraorbital, lachrymal, and mandibular. In counting the pores necessity arises for establishing criteria, some of which are a bit arbitrary. All pores are counted that definitely penetrate, through however small an aperture, into the adjacent canal. Deviations from the basic pattern of 7 preopercular, 7 supraorbital, 4 lachrymal, and 4 mandibular pores are of two types, leading respectively to a reduction and to a proliferation in the number of pores, and since they combine the two types, the deviant populations are excessively variable (as will be seen by an inspection of the tables). Reduction eventuates from a partial to complete failure of the canals and pores to form. Proliferation results both from the interpolation of pores between the standard ones and from the transformation of a single pore into two pores by a disruption of the canal at the position of a pore. This process leads to some uncertainty and arbitrariness in the count, and probably to some inconsistency. It is easy to distinguish a simple round pore not reaching either wall of the canal from two completely separated elements opening in opposite directions into the canal, both edges of which are left free; but there is a continuum of intermediate conditions. We have usually drawn the line at the point where the outer wall of the canal is completely or almost completely disrupted at each edge, but have also given attention to the development of a definite intervening cross ridge. Although decisions are at times difficult, there is a sharp distinction between stocks displaying the standard arrangement and the more extreme forms with marked reductions and proliferations. One limitation of the simple frequency tabulations we have adopted is that it does not distinguish proliferation due to interpolation from proliferation due to disruption; nor does it distinguish between a normal series and one with an open groove between two adjacent pores. A more sophisticated but more elaborate approach, perhaps to be undertaken when the problem is investigated in more detail, would involve distinctions between the different bases for increases or decreases in pore counts.

In counting the pores with precision it is essential to use appropriate magnification, strong illumination, and a fine air jet. When conditions difficult to resolve arise it is often necessary to dampen and then dry the specimen repeatedly.

Another major difficulty stems from the circumstance that the completion of canal and pore formation may be delayed until adulthood. The sequence of formation and completion of the several series is that adopted in the following text, namely, preopercular, supraorbital, lachrymal, and mandibular. By disregarding young specimens this difficulty is not very serious for the preopercular and supraorbital counts, but it does introduce uncertainty into the lachrymal count and even more so into the mandibular count. In part this difficulty has been avoided by utilizing rather comparable series ranging from subadults to large and old adults. But even for the lachrymal and mandibular counts the more extreme variants are readily distinguishable. In a more detailed and sophisticated analysis account should be taken of the stage of the fish's development, and rearing experiments will be needed to determine the phenotypic or genotypic basis for variations in number of pores.

In general, in the far north, the preopercular and supraorbital pores are extremely variable, due to reduction and proliferation, and the lachrymal and mandibular pores are least often developed.

NUMBER OF PREOPERCULAR PORES (Table 16, Fig. 7).—The preopercular canal starts at the pore near the upper end of the preopercle and extends in a rounded right angle to end in a pore behind the mandible, so that there is always a break between the preopercular and mandibular series. Typically, there are 5 intermediate pores, in definite positions. The standard total number, as Gosline (1949:6) indicated, is, therefore, 7. Increased counts may result from the disruption of the canal, stretching one pore into two, but is more commonly the result of the interpolation of a pore, usually near the angle (the upper and anterior ends of the canal are relatively free from variation).

There is a sharp increase toward the far north in variance in the counts of preopercular pores, owing both to reduction and proliferation. Even the more normal counts may involve disruptions. Thus, a count of 7 may represent, instead of the normal complement and arrangement of pores, two sets of crowded pores, say 4+3, separated by a wide interspace occupied by an open canal; or any of various other irregularities (a more sophisticated approach would take such variations into account). To illustrate the extreme individual variability in the pattern of preopercular pores in the north we list, in sequence of frequency, the formulas of specimens from Waquoit Bay (UMMZ 89238) and East Falmouth Beach (CU 16797), Massachusetts (the pores are tallied from above; a plus sign indicates a break

in the series; frequencies are indicated in parentheses): 7 (21), 4+4 (11), 8 (9), 4+3 (8), 0 (5), 4+2+3 (4), 3+2+0 (4), 0+2+2 (4), 4+2+2 (3), 4+5 (2), 4+2+2 (2), 4+0 (2), 9 (1), 2+3+3 (1), 2+2+3 (1), 3+4 (1), 4+2 (1), 3+2 (1), 3+0 (1). Either the number of pores or the formula often differs on the two sides (the sides are independently tallied). The number of variant types exceeds the number of different formulas: for example, the formula 0+2+0 represents three counts of pores 2 and 3 and one count of pores 5 and 6. The mean number of preopercular pores in the New England sample (6.85) departs very little from the standard number of 7, which, however, is represented by only 38 per cent of the sample; increased numbers approximately balance decreased numbers. Variance is the key characteristic.

In southern New England more than one-fourth of the preopercular counts are of 0 to 6 pores, whereas more than 6 were almost always found in specimens of like size from other localities. The specimens examined from Long Island were also extremely variable, though none has fewer than 2 on either side. The Chesapeake Bay samples studied are definitely less extreme; 85 per cent of the counts are of standard number (7), as contrasted with 27.5 and 30 per cent for the Long Island and New England samples, respectively. Within the native range of the species, deviations from 7 to 8 were usually rarely encountered; and deviations to 6 even more rarely, except for the Pecos River samples, for which the ascertained range is 6 to 9, with only 64 per cent at 7. In the Florida Keys and in Bird (Indian) Key the pores are unusually large, completely formed very early, and the 90 counts were invariably 7 (27 specimens in the several series from the Texas coast also exhibited no deviation on either side). Some limited variation is shown by the other Florida stocks examined.

NUMBER OF SUPRAORBITAL PORES (Table 17, Fig. 7).—The supraorbital pores are basically 7, as in cyprinodonts generally (Gosline, 1949), in the following pattern: No. 1, near anterior nostril; No. 2, near posterior nostril; No. 3, about opposite middle of eye; No. 4, at posterior end of nearly straight superior portion of the canal; No. 5, lateral and usually somewhat anterior to 4; No. 6, behind the eye, on the downward segment of the canal; and No. 7, at the lower-posterior terminus of the canal (which has no infraorbital branch in cyprinodonts). A pore may be interpolated at any point, or, more commonly, an increase results from a failure of the canal to roof over completely in the region of a basic pore, which thereby becomes doubled. Reductions stem from an even greater failure of roof formation; very rarely from the failure of a pore to penetrate the roof of the formed canal.

An almost infinite number of pore formulas exists, because (1) any of the pores, except Nos. 1 and 7, may be doubled through the incomplete for-

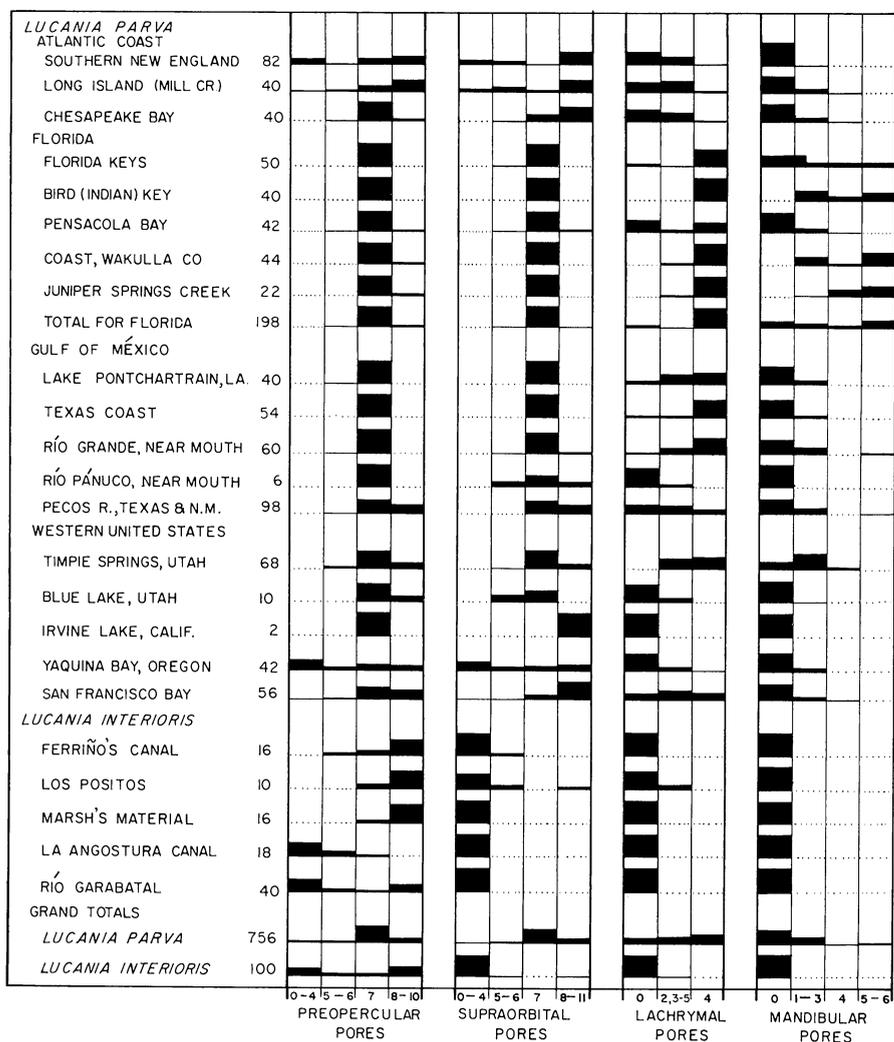


Fig. 7. Geographical variation of *Lucania parva* and *L. interioris* in numbers of cephalic sensory pores, in all four series.

mation of the canal; (2) an accessory pore may open between any adjacent pair of pores; (3) the canal may be broken between any adjacent pair of pores, or between two or more pairs; (4) one pore, or more, may be missing at any such break or breaks. The detailed pore pattern was noted for 750 specimens comprising several series through the indigenous and introduced ranges of the species. This was done to allow a detailed analysis of the variability. To illustrate the variety of formulas, and to indicate the strong

tendency for bilateral uniformity even when the formulas are highly involved, we enter below, in random sequence, the formulas noted for 4 samples from Corte Madera Creek, California. Similar tallies (not included here) for southern New England (UMMZ 89238 and CU 16797) and for near Chesapeake Beach, Maryland (UMMZ 66884), show the same sort of variation, with still other formulas represented, and further illustrate the tendency for bilateral uniformity. This tendency shows that the great variation in pattern is by no means completely random.

In the following list a dash indicates a continuous series with uninterrupted connecting canal; a plus sign indicates a break in the series; and the attached letters (a and b) designate a divided (double) pore. The pores are numbered as indicated above.

Pore Formulas for Collections (CAS 26359 and 26384) from
Corte Madera Creek, California

Left Side	Right Side
*1-2a + 7-8 = 4	1-2a + 7-8 = 4
1-7 = 7; 1-7 = 7 (canal paired)	1-2a + 2b - 3a + 3b - 4a + 4b - 6a + 6b - 7 = 11
*1-2a + 2b - 3 + 5a - 5b + 6 - 7 = 8	1-2a + 2b - 3 + 5a - 5b + 6 - 7 = 8
1-2a + 2b - 3a + 3b - 4a + 4b - 6a + 6b - 7 = 11	(Not countable)
1-3a + 3b - 4a + 4b - 5 + 6 - 7 = 9	1-3a + 4 - 6a + 6b - 7 = 8
†1-2a + 2b - 3a + 3b - 6a + 6b - 7 = 10	1-2a + 2b - 3a + 3b - 4a + 4b - 6a + 6b - 7 = 11
†1-2a + 2b - 3 + 4 - 5 + 6 - 7 = 8	1-2a + 2b - 3a + 4 - 5 + 6 - 7 = 8
*1-2a + 2b - 3 + 4 - 5a + 6 - 7 = 8	1-2a + 2b - 3 + 4 - 5a + 6 - 7 = 8
1-3a + 3b - 4a + 4b - 5 + 6 - 7 = 9	1-3 + 6 - 7 = 5
1-4a + 4b - 6a + 6b - 7 = 9	1-7 = 6 (No. 5 missing)
†1-3a + 4b - 6a + 6b - 7 = 9	1-2a + 2b - 3 + 4b - 6a + 6b - 7 = 10
*1-2a + 2b - 3a + 4 - 6a + 6b - 7 = 9	1-2a + 2b - 3a + 4 - 6a + 6b - 7 = 9
†1-3a + 3b - 4a + 4b - 6a + 6b - 7 = 10	1-4a + 4b - 6a + 6b - 7 = 9
†1-2a + 2b - 4a + 4b - 6a + 6b - 7 = 11 ¹	1-2a + 2b - 4a + 4b - 6a + 6b - 7 = 10
*1-2a + 2b - 3 + 4 - 6a + 6b - 7 = 9	1-2a + 2b - 3 + 4 - 6a + 6b - 7 = 9
†1-3a + 4 - 6a + 6b - 7 = 8	1-3 + 4b - 6a + 6b - 7 = 8
1-3 + 4 - 7 = 7	1-7 = 7
1-2a + 2b - 3a + 3b - 4a + 4b - 7 = 10	1-2a + 2b - 4a + 4b - 6a + 6b - 7 = 10
†1-2a + 2b - 3 + 4 - 5 + 6 - 7 = 8	1-2a + 2b - 3 + 4 - 6a + 6b - 7 = 9
1-3 + 4 - 6a + 6b - 7 = 8	1-2a + 2b - 3 + 3b - 4a + 4b - 6a + 6b - 7 = 11
†1-2a + 2b - 3 + 4 - 6a + 6b - 7 = 9	1-3 + 4 - 6a + 6b - 7 = 8
*1-4a + 4b - 6a + 6b - 7 = 9	1-4a + 4b - 6a + 6b - 7 = 9
*1-7 = 7	1-7 = 7
*1-7 = 7	1-7 = 7
1-6a + 6b - 7 = 8	1-3 + 4 - 7 = 7
*1-7 = 7	1-7 = 7
*1-3a + 3b - 4a + 4b - 6a + 6b - 7 = 10	1-3a + 3b - 4a + 4b - 6a + 6b - 7 = 10
†1-6a + 6b - 7 = 8	1-4a + 4b - 6a + 6b - 7 = 9

* Two sides with identical formulas.

† Two sides with almost identical pattern.

¹ Two pores interpolated between 2b and 4a.

An analysis of all such data, in which the pore pattern is itemized in reference to the individual pores involving 763 counts (the two sides are almost always listed), yields some generalizations regarding the patterns. These generalizations supplement the more complete data on pore counts presented by localities in Table 17 and Figure 7. The detailed analysis shows little regarding regional variation that is not indicated in the analysis of total-count frequencies.

Doubled Supraorbital Pores.—Of the 5421 pores included in this analysis, 351, or 6 per cent, are listed as doubled (though the decision as to doubling is often rather arbitrary; see p. 24). The two next-to-terminal pores are doubled most often and in about equal frequency: No. 2 was so listed 112 times; No. 6, 117 times. Pore 5 is most resistant to doubling (only four counts). Pores 3 (with 50 doublings) and 4 (with 68) are each doubled about half as often as pore 2 or pore 6.

Interpolated Pore.—One pore is interpolated in 26, or 3 per cent, of the 750 counts of canals with pores. Of the 26, twenty were in the interorbital region (between pores 2 and 3 or between No. 3 and 4), whereas only three were in the narial region (between Nos. 1 and 2 or immediately following No. 2) and only three in the postorbital region (between 5 and 6 or between 6 and 7). The variation in this respect, therefore, is greatest medially.

Point where Supraorbital Canal is Broken, Without Loss of a Pore.—Such a break (excluding doubled pores) occurs 104 times (14 per cent of the 750 counts of specimens with pores). The break is most frequent between pores 3 and 4 (in 74 counts); next most often between pores 5 and 6 (in 23 counts); seldom (5 counts) between pores 4 and 5; and very seldom (only one count each) between pores 2 and 3 or between 6 and 7. Again, the variation is greatest in the interorbital region. The rarity of such breaks between pores 4 and 5 and between 2 and 3 and between 6 and 7 is remarkable. No break was observed between the two narial pores (1 and 2). The fact that these pores are definitely related in position to the nostrils and that pore 5 is in a unique location in the alignment of the pores may have a bearing on the limited variation.

When the break involves the loss of one or more pores the pore or pores that are missing occur in the following frequency in the series counted:

Pore (s)	4-5	3-5	4	3	5	2	3-4	6
Frequency	23	7	6	3	3	1	1	1

Again the aberrances are mostly near the middle of the series.

Individual Supraorbital Pores Missing.—The frequency of pores that are missing (when one or more occur) varies widely:

Pore Number	1	2	3	4	5	6	7
Times Missing	28	12	21	48	39	7	9

Obviously the two terminal (postorbital) pores (6 and 7) are least subject to developmental failure; the second narial (pore 2) is almost as conservative; and pores 1, 5, and 4, increasingly in that sequence, are most subject to loss.

Total Number of Supraorbital Pores Missing.—In the 763 detailed enumerations the number of standard pores that are missing (disregarding individual pore identification) varies as follows:

Number of pores missing	0	1	2	3	4	5	6	7
Frequency	675	19	19	16	4	17	0	13

The variation in supraorbital pores follows rather closely that reported for the preoperculars. There is the same increase in variation in the far north, with a complete absence of pores in about one-tenth of the specimens examined from southern New England; still wide, though less, variation on Long Island, with 17 per cent of the counts at 4 (6 is the lowest number observed for any collection from farther south within the natural range of the species, except for one count of 5 from the Florida Keys); and much variation also, for this pore series, in Chesapeake Bay. Again, the Pecos River stock is variable, rather more so than for the preoperculars. None of the Florida Key specimens counted (with the exception of the one count just mentioned), and none examined from Juniper Springs Creek, Florida, deviates from the count of 7; nor did any from Lake Pontchartrain or the Texas coast; but some variation (to 6 and 8) was noted in the specimens from the lower sections of the Río Grande and the Río Pánuco.

NUMBER OF LACHRYMAL PORES (Table 18, Fig. 7).—The pores on the lachrymal (lacrimal, “preorbital”) bone open from a separate segment of the canal system, typically at the dorsal and ventral ends of the subvertical canal and at two intermediate points, each usually at the end of a short, forward-directed side branch. The standard number, therefore, as Gosline (1949:6) noted, is 4. In a considerable number of specimens having 4 pores the canal is broken between pores 2 and 3. Rarely the number of pores is reduced through the failure of the canal to form at one or both ends, and the number is increased in a few specimens by the interpolation of a pore, or by a break in the canal at pore 2 (counting from above) that in effect stretches this pore into two. The dorsal end of the series is definitely more conservative than the ventral end. The canal forms rather late or, in varying proportions at different localities, never forms. In populations with the most delayed development, lachrymal pores tend to develop only in very large individuals. These conclusions are verified in the list of formulas entered below. The tendency for the counts to concentrate at 0 and 4, and also at 2 (for almost invariably any developed segment of canal opens in a pore at either end), militates against any simple statistical treatment.

Thirteen patterns of lachrymal pores were encountered, in varying

frequencies, among the specimens from various localities in which the pattern was annotated. The formulas are based on the identification of the dorsalmost pore as No. 1 and the lowermost as No. 4. Again, a dash indicates that the given pores are connected by a canal; a plus sign represents a break in the canal. The formulas, in sequence of frequencies (indicated in parentheses), are as follows:

1-4 (215); 0 (162); 1-2 (74); 1-2a + 2b-4, with pore 2 divided (45); 1-2 + 3-4 (37); 2-4 (10); 1-3 (8); 1-4, with a fifth pore interpolated near middle of series (6); 2-3 (6); 3-4 (4); 1-2a + 2b-3 (2); 2-4, with a fourth pore interpolated (1); 3-4, with a third pore interpolated (1); pore 2 alone (1); pore 1 alone (1).

Tallies of the formulas by localities seem to show very little that is not indicated by the local differences in total pore number, as shown in Table 18.

From the pore formulas and their frequencies detailed variabilities can be calculated, as is indicated below (following the presentation for the supraorbitals):

Doubled Lachrymal Pores.—Of the 1502 checked, 47, or 3 per cent, are listed as doubled, and pore 2 (from above) is the only one involved.

Interpolated Lachrymal Pore.—One pore was interpolated, near the middle of the series, in only three of the counts.

Point where Lachrymal Canal is Broken.—Except for breaks at a doubled pore, the canal is broken, never with the loss of a pore, and always between pores 2 and 3, 37 times.

Individual Lachrymal Pores Missing.—The frequency of pores that are missing (when one or more occur) varies as follows:

Pore number	1	2	3	4
Times missing	23	6	76	92

The pattern is quite different from that exhibited by the supraorbitals.

Total Number of Lachrymal Pores Missing.—The number of standard pores that are missing (without regard to which pore is involved) varies as follows:

Number of pores missing	0	1	2	3	4
Frequency	303	21	85	2	162

The lachrymal canal and pores usually fail to develop at the extreme north end of the range, and fail to form in about half of the pore series in the populations of Long Island and Chesapeake Bay. About the same proportion characterizes the Pecos River race, in which, alone, the extreme count of 5 is common. A similar proportion obtains about Pensacola Bay, Florida,

to disrupt the usual condition in that state; for the Florida Keys and other Florida key and bay series 84 to 100 per cent of the counts are 4, and for the sample from Juniper Springs Creek all counts are 4 or, occasionally, 5.

NUMBER OF MANDIBULAR PORES (Table 19, Fig. 7).—As in cyprinodonts in general (Gosline, 1949), the sensory canal forms a discrete segment on the mandible, when it develops there (Gosline indicated that *Lucania* is characterized by the absence of mandibular pores, but they commonly do form, in number ranging from 1 to 6, very rarely either 1 or 6). As for the lachrymal, counts higher than 4 may result either from disruption or interpolation.

There is a definite pattern of canal and pores, extending from pore W near the articulation of the mandible forward to pores X and Y and then mesad to the anterior and inner terminus at Z (using Gosline's notation).

Formulas tallied for mandibular pores, utilizing the expressions adopted for the other series, are as follows, with observed frequencies in parentheses: 0 (378); W-Xa + Xb-Z (66, all but 3 in Florida); X-Y (65); X-Z (45); W-Z (23); Y-Z (11); X-Ya + Yb-Z (9); W-Y (4); W-Xa + Xb-Ya + Yb-Z (3, in Florida Keys only); X (3); W-X (2); W-Ya + Yb-Z (1); W + Y-Z (1); W-Z, with W doubled (1); W (1); Z (1).

The number of times individual pores were doubled, in the 236 counts with one or more pores, is: W (1), X (71), Y (13), Z (0). No interpolations occurred. The canal was broken in only one count, between pores W and Y (with X missing). The individual pores that are missing are as follows:

Pore	W	X	Y	Z
Times missing	134	14	7	75

The series, therefore, is best developed medially, least well at the posterior end. The total number of pores that are missing varies as follows:

Number of pores missing	0	1	2	3	4
Frequency	94	59	78	9	378

The mandibular pores are typically absent in samples from the northern and central sections of the Atlantic coast of the United States. The extreme condition obtains in southern New England, from which area only one count, of 2, other than 0, was obtained. Failure to form mandibular pores is indicated by our counts to be usual also at most other localities. In the seemingly weakly developed race of interior Florida, as represented by the series from Juniper Springs Creek, the modal number is 5, with a range from 3 to 5. In two other Florida series, from near the coast of Wakulla County and from Bird (Indian) Key, all specimens examined have at least 2 mandibular pores, and 5 pores occur more often than, or almost as often as, 4.

MORPHOMETRIC VARIATION

Regional differences are exhibited by morphometric as well as by meristic features. Again, the differences are probably in part phenotypic, in part genetic. In respect to sexual dimorphism, in the expanse of the fins and in other features, the environment, as is indicated below, plays a dominant role.

LENGTH OF PELVIC FIN (Table 21).—The length of the longer pelvic fin, measured from the extreme structural base to the very tip, is expressed as the number of times and estimated tenths that it is stepped, with dividers under magnification over the body surface, into the predorsal distance (from the extreme anterior end of the dorsal-fin base to the front of the upper lip). On these criteria the ratio can be duplicated by different persons.

This character, although of prime value in distinguishing *Lucania interioris*, is also significant within *L. parva*. The pelvic (like the other fins) averages longer in adult males than in adult females, but the degree of sexual dimorphism varies greatly with the stock. In some collections, as those from the far north (southern New England and Long Island), Florida Keys, Pensacola Bay, and Lake Pontchartrain, there is little overlap in the ratios, whereas in other series, as those from Texas (including the coast, the Río Grande mouth, and the Pecos River), there is only a slight average difference; in other series, including the one from Chesapeake Bay, an intermediate condition prevails, to break the regularity of the cline.

There are strong reasons, however, for believing that, within the limits of genetic expressivity, the degree of sexual dimorphism is directly dependent on the environment. Under depauperating conditions, as in small indoor aquaria, many cyprinodonts and other fishes fail to develop the full flower of secondary sexual characters. Great differences in sexual dimorphism are exhibited by two populations of *Lucania parva* that are seemingly, as is argued below, of the same stock. The Pecos River race is characterized, along with other Texas populations examined, by a remarkably slight, only average, difference between the sexes in the length of the pelvic (and other) fins. The supposedly derived stock of Timpie Springs, Utah, in contrast, shows almost no overlap in this character. In this population the pelvic fins are more strikingly enlarged than in any series studied from within the natural range of the species, with the probable exception of the sample from Bird (Indian) Key in Florida. Other secondary sexual characters are also exaggerated, in striking contrast with the conditions holding in the Pecos River (Pl. II). Some unfavorable aspect of the native environment seems to depress the male characters, whereas something in the adopted home leads to their extreme exuberance.

DEPTH OF BODY (Table 22).—The depth of the body is expressed as the number of times the greatest depth (below origin of dorsal fin) is stepped

with dividers over the body surface from the front of the upper lip to the structural base of the caudal fin. High males and ripe females are both deep-bodied, and, prior to senility, the depth increases somewhat with age. In some collections males average deeper than females; in other series, slenderer. Initial separate tabulation seemed to serve no better than the combined figures, which are therefore presented.

The range of this ratio is indeed great, from 2.7 to 4.5; the modes range between 3.0 and 4.0. The body averages only slightly deeper along the Atlantic Coast of the United States than along the Gulf Coast west of Florida, and no general cline seems to exist. Within Florida, however, an extensive cline is exhibited, grading from extreme depth (and subrhombic body outlines) in the Florida Keys to extreme slenderness (and more rounded contours) in the interior, freshwater populations (Table 22, Pl. I). In view of this vast difference and its association with various meristic differences, pointed out above, it is considered highly probable that the differences are at least in large part genetic. However, as already noted, the problem is one that calls loudly for experimental attack.

PROPORTIONAL MEASUREMENT OF PREDORSAL LENGTH (Table 23).—This measurement was made from the extreme front of the base of the dorsal fin, as determined by inserting the sharp point of dividers, to the front of the upper lip. The sexes are separately tallied.

The data are combined in Table 23 for all localities of the species, as the regional variation is very minor, with broad overlaps between all series. Since the abdomen averages proportionately a little longer and the dorsal fin a bit shorter in females, the ratio averages slightly lower than in males.

PROPORTIONAL MEASUREMENT OF DISTANCE BETWEEN ANAL ORIGIN AND CAUDAL BASE (Table 24).—This measurement was made from the extreme structural base of the caudal fin on the midline of the body to the extreme front of the base of the anal fin, as determined by inserting the sharp point of dividers (inside the genital pouch for females), and pressing gently against the fin. The sexes are tallied separately.

This measurement, as in many other fishes, averages shorter in females than in males, because their abdomen is longer and their urosome correspondingly shorter (compare data in Table 24, in boldface type for males and in italics for females). The proportion, expressed in hundredths of standard length, varies widely in *L. parva*, from 37 to 45 for males and from 34 to 44 for females. The values differ considerably with locality. The data indicate a cline from the lowest values in the far north to the highest values along the Gulf of Mexico, with a decrease again, on the average, in the rather distinctive Pecos River race.

OTHER PROPORTIONAL MEASUREMENTS (Table 25).—Fourteen body and head proportions were measured in small to medium series of males and

females from seven localities within the native range of *Lucania parva* (and from two Western localities where the species has recently become established; also from the five series of *L. interioris*). The measurements were made as indicated by Hubbs and Lagler (1958), or as stated above. The "interorbital width" is the least fleshy distance, at the front of the top of the orbit. The dorsal- and anal-fin lengths are from the extreme front base to the farthermost tip.

Average sexual differences are indicated for the following characters (with the direction of the dimorphism in males indicated by a plus or minus sign in parentheses): predorsal length (-); anal origin to caudal base (+); caudal-peduncle depth (+); head depth (+); head width and interorbital width (usually slightly less); orbit length (+, probably because males average smaller than females); all fin lengths (+).

Geographic trends for some of these proportional measurements have been treated on preceding pages, and are in general here confirmed. Other trends and distinctions are brought out in the following discussion of populations.

DISCUSSION OF LOCAL VARIANTS

Having now considered variations displayed by *Lucania parva* in each of the characters utilized, we are prepared to discuss the local variants. These are relatively numerous and diverse, with notable differences between the local forms as well as wide individual variation within each form. This high degree of variation is concordant with the vast latitudinal range of the species, from southern Massachusetts to the Río Pánuco in northeastern México, and with the wide spectrum of habitats (as shown by the studies of Beck and Massmann, 1951; Kilby, 1955; Kilby and Caldwell, 1955; Simpson and Gunter, 1956; Clark Hubbs, 1957; Renfro, 1960; Springer and Woodburn, 1960: 25; and others). The high geographical variation is consonant also with the relatively localized habits of the species (though according to Beck and Massmann, 1951, it does undertake mass movements in estuaries); there is no evidence that it has colonized the Bahama Islands or any of the Antilles.

This discussion of the local forms is essential to the later discussion of the probable source of the stocks that have suddenly become established at five places in the western United States, and is significant also in the discrimination of *Lucania interioris*, the isolated endemic in the Cuatro Ciénegas Basin of Coahuila, México.

SOUTHERN NEW ENGLAND.—One of the most trenchantly distinct of the local forms inhabits southern New England (represented by several collections from southern Massachusetts). This is not surprising, in view of its peripheral location at the northern limit of the species and near the north-

ern extreme for the family, where severe climatic conditions are encountered. Were it not for the broad area of intergradation with more southern types and the irregularity in the clines, this New England race would warrant separation as the nominate subspecies (*Lucania parva parva*). This speciation situation strikingly parallels that in *Cyprinodon variegatus* Lacépède, which also ranges from southern New England to eastern México and is represented along a limited coastline in the northernmost section of its range by a local differentiate, *C. v. ovinus* (Mitchill), which is separated from southern populations by a broad band of irregular intergradation (Hubbs, 1936:223-24). Among other estuarine fishes that exhibit a more or less similar pattern of differentiation we note:

Anchoa mitchilli (Valenciennes).—Hubbs and Perlmutter, 1942:583, fig. 1; Hubbs and Hubbs, 1953:50-51, figs. 1-2; Hildebrand, 1943:87-94; 1964:178.

Fundulus heteroclitus (Linnaeus).—Jordan and Evermann, 1896:640-41. A case in need of further study (Hubbs, 1926:8). Not including *F. grandis*, which is specifically distinct (Miller, 1955:7-8).

Menidia beryllina (Cope) and *M. menidia* (Linnaeus).—Kendall, 1902; Jordan and Hubbs, 1919:50-54; Gosline, 1948.

Trinectes maculatus (Bloch and Schneider).—Jordan and Evermann, 1898:2701; Hubbs, 1932a; Carl L. Hubbs and John A. Bollinger, MS.

All of these speciation clines, however, call for more critical statistical analysis, and particularly for experimental attack; rearing experiments, indeed, may show that the characters involved are largely or even wholly phenotypic.

In the analysis of the southern New England form of *L. parva*, full data were taken on one collection (CU 16797), from East Falmouth Beach, Massachusetts, and supplementary data were derived from various other localities in southern Massachusetts, for the numbers of dorsal and anal rays and of gill rakers, and for the body-depth, predorsal, and anal-to-caudal measurements. The general proportional measurements (Table 25) were taken on a series (UMMZ 89238) from Waquoit Bay, Massachusetts.

A prime distinguishing feature of the northernmost form of *Lucania parva* is the increased number of gill rakers, as detailed in the text on page 22, in Table 20, and in Figure 5. Most (84 per cent) of the specimens have 9 to 12 rakers, rather than 4 to 8 as in the southern populations.

About equally striking is the frequent reduction and increased variability in the pores of the sensory system of the head, owing to incomplete development and occasional lack of canals and pores and to irregular interpolation of pores. This is the only race, within the native range of the species, in which the preopercular and supraorbital pores were found to be reduced in more than occasional variants below the standard number of 7, and the only one in which these pores were found to be totally lacking in

some specimens (Tables 16 and 17, Fig. 7). In this race the lachrymal pores are more frequently reduced in number or absent than in any other examined (Table 18, Fig. 7), and it is the only one in which the mandibular pores (and canal) are absent in almost all specimens examined (Table 19, Fig. 7).

Other characteristics help to distinguish the southern New England race. One such is the shortening of the urosome; the distance from the origin of the anal fin to the base of the caudal (Table 24) in adult females is usually less than 0.38 of the standard length. Correlated with this is the average reduction of the number of anal rays (Table 4, Fig. 2), as compared with most southern populations. On similar comparison the body is relatively deep (Table 22), in correlation with which the counts of scales between dorsal and anal fins, around the circumference of the body (Fig. 5), and around the caudal peduncle are relatively high (Tables 12–14).

LONG ISLAND.—The Long Island stock of *Lucania parva*, as represented by a sample from Mill Creek, below bridge at Watermill, on Macalf Bay, Suffolk County, New York (CU 26849), is essentially like the southern New England race in the high number of gill rakers (Table 20, Fig. 5), the deep body (Table 22), and the high number of scales in transverse counts (Tables 12–14), but approaches the more southern stocks in the development of cephalic sensory pores (Tables 16–19, Fig. 7) and in the length of the urosome (Table 24), and resembles most southern stocks in having the anal rays (Table 4, Fig. 2) more frequently 10 than 9. The sample from Long Island probably corresponds most closely with the typical race of *Lucania parva*, for the type locality of *Cyprinodon parvus* is cited by Jordan and Evermann (1896:666) and others as Greenport, Long Island (on the basis of Baird's statement, 1855:345, that "I observed it, sparingly, in many localities in Long Island, especially at Greenport").

CHESAPEAKE BAY REGION.—The next stock sampled, progressing southward, is that of the Chesapeake Bay region. Most of the data were taken from a large series (UMMZ 66884), seined from a creek near Chesapeake Beach, Maryland; supplementary determinations (dorsal- and anal-ray and gill-raker counts and body-depth, predorsal, and anal-to-caudal measurements) were derived from specimens from various other localities in the region.

In several respects the Chesapeake Bay type is intermediate between the more northern stocks and those around the Gulf of Mexico (excluding Florida). This is particularly noteworthy for the gill-raker number (Table 20, Fig. 5) and for the anal-to-caudal distance (Table 24). The anal rays average fewer than in southern New England and about the same as in coastal Florida, but lower than around most of the Gulf of Mexico.

The evidence from the cephalic sensory-pore characters (Tables 16-19, Fig. 7) is various: the preopercular pores are less variable here than farther north, but are not quite so consistent as they are in the south; the supraorbitals are variable, as they are farther north, but in none of the specimens examined are they absent, as they are in some from southern New England; progressing southward, the only form with like variability is that of the Pecos River. The lachrymal- and mandibular-pore pattern is less distinctive.

The body averages slightly slenderer here than farther north, about the same as in most of the stocks around the Gulf of Mexico (Table 22). The counts of lateral scale rows and of scales from dorsal to anal (Tables 11-12) are average; the body-circumferential and caudal-peduncular scale counts (Tables 13-14) are high, about as to the northward.

On the basis of available evidence the overlap in all characters with stocks to the north and to the south is so extensive as to discourage thoughts of subspecific separation, even on the assumption that the differential characters have a genetic basis.

NORTH CAROLINA.—The one small sample from North Carolina was investigated only for dorsal and anal rays (total counts) and for the predorsal and anal-to-caudal measurements. None of these proved of marked significance, except that the anal-to-caudal measurements (Table 24) continues the southward positive cline. Despite the extreme paucity of variational data for the long stretch of coastline intervening between Chesapeake Bay and Florida, we feel rather confident, albeit on the rather subjective basis of examining numerous collections from the intervening area, that *L. parva* is relatively constant there in characters and in habitat.

FLORIDA.—Under the discussions of the various characters frequent reference was made to the phenomenal diversity exhibited within Florida, exceeding that in the entire remainder of the wide range of the species. This is somewhat of an enigma, but is in line with the well-authenticated high incidence of endemism in the Florida peninsula. The wide regional variation in some characters in Florida, for instance in the number of vertebrae (see below), appears, in view of relative constancy elsewhere under a wide variety of temperature and other conditions, to be at least partly genotypic. In view of the clear evidence that much of Florida was submerged during parts of the Pleistocene period it is possible that the differentiation was rapid. Alternate flooding and emergence may have played a role in the speciation drama.

None of the Florida races has received a species-group name, though Jordan (1884:109) and Jordan and Evermann (1896:666) took the extreme variant of the Florida Keys, erroneously, to represent *Lucania parva*, as distinguished from *L. venusta*. None of the Florida forms exhibits any distinc-

tive approach toward the interior forms of other regions, namely the Pecos River race of *L. parva* and the Mexican species *L. interioris*.

We have taken data from a considerable number of collections. These we group into apparently natural and more or less homogeneous classes, which are listed below in the usual sequence shown by the clines in their characters. The series studied are as follows:

1. The Florida Keys (extending southwestward from the tip of Florida; in Monroe County): UMMZ 65265, Key West (collected by David Starr Jordan); UMMZ B61-46, bay on Crawl Key; UMMZ B61-48, Big Pine Key; UMMZ B61-64, Shell Key, in mangrove channel; USNM 197410, ocean side of Matacumbe Key (Pl. I).

2. Bird (Indian) Key: USNM 184225, in Boca Ciega Bay at St. Petersburg.

3. Bays and other keys on the west coast: UMMZ 65236 and 86301, Big Gasparilla Key; UMMZ 65934, Pine Key; UMMZ 109981, Anna Maria Key; UMMZ 113260, Lemon Bay. Only a few characters studied.

4. Pensacola Bay: chiefly UMMZ 136550, Pensacola; plus a few counts of dorsal and anal rays and a few measurements of body depth and of the predorsal and anal-to-caudal distances on UMMZ 61447 and 65286, Pensacola, and 111836, Santa Rosa Island (Pl. I).

5. Coast, Wakulla County, on the Florida panhandle: collections in UMMZ from the St. Marks Migratory Bird Refuge, detailed by Hubbs, Walker, and Johnson (1943:8-9). Only a few characters studied (data largely abstracted from the 1943 paper).

6. Mill Creek, vicinity of Bradenton: UMMZ 109953 and 111788. Only a few characters studied.

7. Slough of St. Johns River, west of Indian River City, Brevard County: UMMZ 113233. Freshwater vegetation recorded. Only a few characters studied.

8. Salt Springs Creek, 30 miles northeast of Ocala: UMMZ 110609. Water recorded as "slightly salty," with pH 8.

9. Juniper Springs Creek, at Sweetwater Springs, 35 miles east of Ocala: UMMZ 110672. Water recorded as "slightly salty," with pH 7.6.

Although for many of the characters the analysis is confined to the series from the Florida Keys, Bird (Indian) Key, Pensacola Bay, and Juniper Springs Creek, the data taken in all regions, along with a cursory examination of yet other series, lead us to believe that clines in many characters are marked and general (Pl. I).

The most striking difference (noted only for the four main regions of study) is found, unexpectedly, to lie in the vertebral number (Table 15, Fig. 6), which varies from a mode of 26 in the Florida Keys to a mode of 29 in Juniper Springs Creek, with nicely intermediate values at Bird (Indian) Key and in Pensacola Bay (see further discussion, p. 22).

About equally striking, and of course much more obvious, are the great differences in body depth (Table 22, Pl. I), grading in the conventional stepped ratio from a mode of 2.9 or 3.0 in the very deep-bodied, subrhombic Florida Keys race to 3.7 in the less rhombic Juniper Springs Creek collection (which in several respects is the most extreme of the freshwater interior races); however, the cline is a gradual one.

Along with the difference in body shape is a very striking difference in coloration, grading from almost wholly plain and light in the Florida Keys to rather strongly dark-blotched in the interior (Pl. I). The slenderer body and the blotched pattern of the interior stocks, along with a trend toward a larger eye and a wider and flatter interorbital, are juvenile characters, but other features are not.

Correlated with the positive cline in vertebral number, we find that the rays in the several fins increase in number in the sequence of localities from the Florida Keys to the interior (Tables 2–8, Figs. 2 and 4). The changes in mode are from 11 to 12 for the dorsal, from 9 to 10 for the anal, and from 13 to 14 for the pectoral; there is probably a slight positive cline also for the caudal.

The trends for scale counts (Tables 11–14, Fig. 5) are various. The number of lateral rows, following closely the cline in vertebral number, shifts from 25 to 28. For the dorsal-to-anal, body-circumferential, and caudal-peduncular counts, however, the situation is quite different; the Florida Keys and Juniper Springs Creek series are essentially alike, whereas the Pensacola Bay type, like populations from farther west in the Gulf of Mexico, has reduced numbers.

Similarly, the trends for the cephalic-pore counts (Tables 16–19, Fig. 7) are various. The preopercular and supraorbital pores are large, regular, and consistent in number and are formed early in the Florida Keys, Bird (Indian) Key, and Juniper Springs Creek lots; they are slightly variable about Pensacola Bay. The lachrymal pores are more frequently lacking about Pensacola Bay than on the Florida Keys and on Bird (Indian) Key, and are present in all specimens examined for this character in the Juniper Springs Creek collection. The mandibular pores are often lacking in the Florida Keys and Pensacola Bay series, but are more consistent, never lacking, and numerous (usually, and uniquely, 5) in the Juniper Springs Creek sample. In the Bird (Indian) Key and Wakulla County coastal samples the range is from 2 to 5, with modes at 3 and 5.

The gill rakers (Table 20, Fig. 5) exhibit fluctuations in average numbers and in range, with no obvious cline.

The Pensacola Bay samples stand somewhat apart from the cline just discussed in several characters, in which, understandably, they approach the samples from the Gulf Coast still farther west.

GULF OF MEXICO COAST WEST OF FLORIDA AND NORTH OF THE RÍO GRANDE.—The numerous stocks examined from this wide area seem fairly consistent, strikingly so in comparison with the rampant variance in Florida. The samples more completely analyzed (with supplementary data from

other localities for dorsal and anal rays, body depth, and predorsal and anal-to-caudal distances) are as follows:

1. Lake Pontchartrain, Louisiana, in roadside ditch, Orleans Parish: UMMZ 155316.
2. Coastal Texas, at Ninemile Point (UMMZ 179912, from UT 767) and Ninemile Pond (UMMZ 179913, from UT 787), 9 miles north of Rockport, Texas. These collections came from near the type locality of *Limia venusta* (Indianola, Calhoun County).

The "Texas coast" specimens (4 males) utilized for full measurements in Table 25 comprise one from Brazos Island, Cameron County (UMMZ 111038), and three from Olmito, Cameron County (UMMZ 157339), near the mouth of the Río Grande.

General consistency through the area is illustrated by the determinations made on various series from the coastal regions of Alabama, Mississippi, Louisiana, and Texas, namely for the number of dorsal and anal rays (Tables 2 and 4), which are modally 11 and 10, respectively, and for the predorsal and anal-to-caudal measurements (Tables 23 and 24). The anal-to-caudal dimension is high for the species as a whole, but only on the average.

The other characters, determined in detail only for Lake Pontchartrain, Louisiana, and from near Rockport, Texas, are rather average for the species and allow the following further characterization of the Gulf coastal form (*venusta*): caudal rays modally 16; pectoral rays modally 13 (Lake Pontchartrain) or 14 (Texas); lateral scale rows modally 27; dorsal-to-anal scale count modally 9; body-circumferential scale count modally only 21 or 22; peduncular scale counts widely scattered from 12 to 16; vertebrae averaging 27.7 (Lake Pontchartrain) or 28.2 (Texas); preopercular pores almost always 7; supraorbital pores consistently 7; lachrymal pores modally 4, but variable; mandibular pores usually absent, occasionally 2 or 3, but not 4 or 5; gill rakers with a wide spread of counts from 6 to 9; pelvic fin of average length for the species; body depth (measured on Texas series only) also average.

RÍO GRANDE NEAR MOUTH.—There are some indications of slight differentiation in the Río Grande at and near its mouth (the type locality of *Lucania affinis* Girard, 1859b:118–19). The species is common near the mouth, and ranges for a considerable distance upstream (Robinson, 1959, and Clark Hubbs, personal communication). The following small collections were utilized:

1. Brownsville, Cameron County, Texas; collected August 9, 1952: SIO 62-264-27A.
2. Tributary to Río Grande 7.7 miles east of Brownsville; April 9, 1952: UMMZ 167634.
3. Arroyo Tigre Grande, at Highway 83, Zapata County, Texas; February 26, 1955: UMMZ 179916 (from UT 4729).

As already noted, there seems to be some inconsistency in the anal-ray counts (Table 4, Fig. 2) for this grouping, since 9 predominates in two

collections, as in the Pecos River race, and 10 in a third series (as along the Gulf Coast generally); for the combined lot the anal-ray count is intermediate between the counts for the Texas coast and for the Pecos River. The dorsal-ray count (Table 2, Fig. 2) is also intermediate, but the differences are less sharp. The dorsal-to-anal scales (Table 12) seem to average a bit higher than in either of the other series and the gill rakers (Table 20, Fig. 5) average slightly fewer. In other respects agreement is close with the populations inhabiting the Gulf of Mexico coast west of Florida and north of the Río Grande. The differences may prove untenable on further study, but there is some suggestion that the population near the mouth of the river either is affected by fish of a different type dispersed down the river from above, possibly even from the Pecos River, or is somewhat differentiated, on either a genotypic or a phenotypic basis.

RÍO PÁNUCO NEAR MOUTH.—Two collections, though totaling only 3 specimens, show that this species, like a number of other North American types, ranges southward into northeastern México. One female (UMMZ 180041), 19.7 mm in standard length, was collected on February 3, 1937, by J. Mortimer Sheppard in a small, swampy drainage ditch tributary to the Río Tamesí (of the Río Pánuco system), 5 miles above the mouth of the Tamesí at Tampico. Two small males (TU 5634), 17.1 and 17.7 mm long, were taken by R. M. and J. H. Darnell and E. Liner in the lower Tamesí drainage, in Laguna de Chairel, at Tampico, on December 29, 1952 (Darnell, 1962:329). Counts and selected measurements were taken on all 3 specimens; full proportional measurements on the female.

All earlier inclusions of *L. parva* in the Mexican fauna (as by Meek, 1904:109; Regan, 1907:80–81; and de Buen, 1940:29; 1947:276) were apparently based solely on the type specimens of *L. affinis* from near the mouth of the Río Grande. It seems probable, on *a priori* grounds and by analogy with the distribution of other species, however, that *L. parva* ranges through the Laguna Madre and other coastal lagoons of northeastern México, which extend from near the Río Grande to about 80 km south of Tampico, and, therefore, that the stock in the lower Pánuco system is at least very similar to that of the Gulf Coast of the United States. The very limited material from México is barely indicative of the relationship that exists. In most characters the agreement seems close. Average differences—the low caudal-ray count, the poor development of lachrymal and mandibular pores, the slender body, the short snout, the large eye, and the small vertical fins—may be attributable to the small size and probable youth of the specimens. However, the possibility remains that the southernmost population may be represented by a dwarf form with juvenile characteristics.

The species presumably does not range farther south than the lagoons south of Tampico. The highlands that impinge on the coast between these

lagoons and the Veracruz plains appear from our studies to constitute a barrier that rather effectively separates the predominantly Nearctic and Middle American lagoonal and freshwater faunas.

PECOS RIVER, TEXAS AND NEW MEXICO.—Numerous collections, mostly in The University of Michigan Museum of Zoology and The University of Texas, dating from 1938 to the present, attest the abundance of *Lucania parva* in the middle and lower course of the Pecos River, in Texas and New Mexico, from which areas it has been reported by Clark Hubbs (1954:285) and Koster (1957:83). Along with *Fundulus zebrinus* Jordan and Gilbert, *Cyprinodon* sp., and other salt-tolerant fishes, it inhabits the highly mineralized portion of the Pecos, but not the upper headwaters. The salinity of its habitat in the Pecos has been indicated by Clark Hubbs (1957:99). The Pecos population appears to be a disjunct unit, although during floods individuals may well be carried downstream through the Río Grande, where the species seems to occur only in the lower part of the basin. The possibility that such expatriates may be modifying the lower population is mentioned on preceding page. The occurrence of this interior stock is of especial interest in connection with the discovery of *Lucania interioris* in an interior drainage basin in Coahuila, México.

The characters of the Pecos population indicate that it probably represents a distinct race of *Lucania parva*, with no definite approach toward *L. interioris* (as is specified in the account of that species), nor toward the interior races of Florida. Oddly, the Pecos race in some characters approaches the northernmost race (of southern New England), but not succinctly enough to lend much weight to the idea that the Pecos form may be a northern relict of Pleistocene origin. In some characters this form contrasts rather sharply with those of the far north. The more significant characters and relations of the Pecos race are compared in Table 26 with those of other races of *L. parva* (disregarding in this connection the diverse types of Florida). This comparison is introduced in connection with the presentation below of evidence that the Pecos River stock was the source of the fortuitous introduction of the species into three localities in the western United States.

ESTABLISHMENT OF *LUCANIA PARVA* IN WESTERN UNITED STATES

Beginning in 1958, perhaps earlier, *Lucania parva* has unexpectedly and almost mysteriously appeared in five well-separated locations in the western United States, far outside its native range. The places, in order of first collecting, are: the region about San Francisco Bay, California; waters about Yaquina Bay, on the Oregon coast; Timpie Springs, in the bed of Pluvial Lake Bonneville, Utah; Blue Lake, in the same lake bed and state; and Irvine Lake, a reservoir in southern California (Fig. 1). We first record the

evidence for the establishment of the species in each location and then attempt to explain how the introductions, all undocumented, probably occurred. The extensive establishment of *L. parva* in the West is consonant with its wide ecological tolerance.

SAN FRANCISCO BAY, CALIFORNIA

According to data furnished by W. I. Follett, E. W. Kirschbaum, William A. Newman, Howard O. Wright, and others, captures of *Lucania parva* around San Francisco Bay (Fig. 1, insert) have been as follows, in chronological order:

"Not later than the spring of 1958" (date not recorded), Wright reports that the species was taken at Aquatic Park, Berkeley, near the shore of San Francisco Bay. It was associated there with a recently introduced Asiatic shrimp, *Palaemon macrodactylus* (Rathbun).

May 18, 1958, Wright collected specimens in Richmond Tidal Slough (north of Berkeley, on the east side of San Francisco Bay), at 37° 55' N. Lat., 122° 20' W. Long., in fresh water. One of the specimens, an adult male 26 mm long, is in the California Academy of Sciences (CAS 26355).

November 28, 1958, Kirschbaum, with David Rentz, dip-netted specimens (5 preserved, CAS 26357) in the lower, brackish course of Corte Madera Creek, Marin County, on the west side of the northern area of San Francisco Bay.

June 27, 1959, Kirschbaum, with Anthony Diver, seined hundreds of specimens (14 preserved, CAS 26359) in the same creek, beginning 0.8 km below Kentfield Bridge and continuing downstream toward the bay. With the possible exception of the topmelt, *Atherinops affinis affinis* (Ayres), *Lucania* was the dominant fish. The specific gravity of the creek was determined as 1.011, but transfers to fresh water (1.001) and to normal sea water (1.025) induced no ill effects. The stream had a mud bottom and contained thick masses of floating algae, leaf litter, etc. Other associated fishes were sticklebacks, *Gasterosteus aculeatus* Linnaeus, and gobies, *Eucyclogobius newberryi* (Girard), *Gillichthys mirabilis* Cooper and *Clevelandia ios* (Jordan and Gilbert); also the introduced shrimp *Palaemon macrodactylus*.

October 10, 1959, Kirschbaum, with Rentz, seined 114 additional specimens in the same creek (CAS 26384).

December 6, 1959, Kirschbaum, Diver, and Rentz dip-netted many additional specimens in Corte Madera Creek and in the lower reaches of Mill Valley, tributary to Richardson Bay, also in Marin County (specimens in California Academy of Sciences).

Summer of 1961, Wright found *Lucania* in Lake Merritt, freshwater lake in Oakland, in open connection with San Francisco Bay, again in association with *Palaemon macrodactylus*.

January, 1962, Newman dip-netted about a dozen specimens of *Lucania* about pilings in Palo Alto Yacht Harbor, South San Francisco Bay, once again in association with *Palaemon macrodactylus*.

It is obvious that *Lucania parva* has become well established about San Francisco Bay and contiguous waters, with vast increase in numbers and in range.

All of the San Francisco Bay specimens studied by us came from Corte Madera Creek and Mill Valley.

YAQUINA BAY, OREGON

According to Carl E. Bond and associates of Oregon State University *Lucania parva* appeared in waters contiguous to Yaquina Bay during about the same period as in San Francisco Bay:

July 26, 1958, an adult male (OSU 321), and August 2, 1958, two adults (OSU 322), taken by Leonard R. Coleman and George Chadwick in a slough off the bay, in a small pool about 0.75 m deep near the upper limit of tidal influence. In this spring-fed pool the salinity is known to vary with the tide from 3.0 to 26.7 ‰. Water temperature on August 2 was 19.5° C. The bottom was foul-smelling black mud. Associated animals were a shrimp, *Crago nigricauda* (Stimpson), and six fishes: *Oncorhynchus kisutch* (Walbaum), *Clevelandia ios* (Jordan and Gilbert), *Leptocottus armatus armatus* Girard, *Cottus asper* Richardson, *Gasterosteus aculeatus aculeatus* Linnaeus, and *G. a. microcephalus* Girard. Channels through the mudflat near this pool had been visited 13 times, and many fishes collected, between February and July 26, 1958, without encountering *Lucania*.

October 9, 1958, 3 specimens (OSU 388) collected by Chadwick in Johnsons Slough, off the bay.

November, 1960, 3 half-grown and 10 adults collected by Wilber P. Breese in Kings Slough, off the bay.

March 28, 1963, 15 specimens collected for us about Yaquina Bay by Breese.

It seems obvious that *Lucania parva* has become well established about Yaquina Bay, as well as about San Francisco Bay. Since no specimens had been taken previously about the bay by the staff of Oregon State University, which maintains a fisheries laboratory there, or by Hubbs and Schultz in 1926, it is probable that the species was rather recently established, or had only recently multiplied sufficiently to be taken.

The establishment of the species in ditches tributary to Yaquina Bay was mentioned by Bond (1961:32).

TIMPIE SPRINGS, UTAH

April 11, 1959, 14 adults (UMMZ 175953) taken by Guy G. Musser.

August 10, 1960, large series of young to large adults (UMMZ 178651) taken by Miller and party.

This large, cool spring, dammed to form a sizable pond, lies just above U. S. Highway 40 in Tooele County, only slightly higher than the marshes around the south shore of Great Salt Lake, and therefore well within the bed of ancient Lake Bonneville. It issues at the temperature of 18° C from crevices in travertine and spreads over a meadow area in the mouth of Skull Valley, just east of the settlement of Timpie, about 23.3 km north of Iosepa, in the NE corner of T. 1 S, R. 8 W. The spring was known as Big Spring

when Hubbs and party collected fishes there on June 7, 1942. It was named Salt Spring on the map of Carpenter (1913:pl. 2), who labeled a spring somewhat farther east as Timpie Spring.

It seems virtually certain that *Lucania* was introduced very recently into Timpie Springs. The collection of June 7, 1942, comprised four liters of *Gila atraria* (Girard) but no introduced fishes were noted. Although the spring pond had been used since 1954 by Arden R. Gaufin of the University of Utah for field work in limnology prior to the first capture of *Lucania* on April 11, 1959, no specimens of this cyprinodont had been collected or observed among the introduced fishes. The collection of August 10, 1960, contained, in addition to the one native fish (*Gila atraria*) and the introduced *Lucania*, which was common in the deep water about the spring inlets, an abundance of mosquitofish, *Gambusia affinis affinis* (Baird and Girard), mostly around the marshy edge of the pond, largemouth bass, *Micropterus s. salmoides* Lacépède and bluegills, *Lepomis m. macrochirus* Rafinesque.

Having heard that largemouth bass fingerlings from Texas had been stocked in Utah, information regarding the source of the largemouth bass in Timpie Springs was sought from the Utah Department of Fish and Game and from the federal fishery station at Springville, Utah. Donald C. Hales of the state department wrote on March 1, 1963, that bluegills (*Lepomis macrochirus*) were stocked in Timpie Springs in 1952 and 1953, with no record of the source. Further, ". . . Mr. Marion Madsen, our former Chief of Fisheries, . . . stated that he stocked some largemouth bass [in Timpie Springs] in 1947 or 1948. These fish were reared at the Federal hatchery at Springville, Utah. In so far as I can determine, the Federal Government has been our only source of supply for bluegill and largemouth bass since the 1947 or 1948 plant. Mr. John Thompson, Superintendent of the Springville Federal Hatchery, informs me that the bass stocked in 1960 came from Santa Rosa, New Mexico."

John A. Thompson, Manager of the Springville Station, wrote, on August 28, 1962, as follows: "In September 1944, Tooele Wildlife Federation received 5,000 Bluegills for Mill Pond. I do not know if Mill Pond is near Big Springs [the alternative name for Timpie Springs]. The bluegills were from Dexter, New Mexico.

"On November, 1952 delivered to Tooele Wildlife Federation 100 L. M. Bass and 1,000 Bluegills at Grantsville, Utah for Big Springs. The fish were reared at the Springville Station, also 200 L. M. Bass and 2,000 bluegill sunfish were delivered at the same time for Clear Lake.

"All the bass planted from this station are hand counted and we have never seen any Rainwater Fish (*Lucania parva*)."

It is thus indicated, as Sigler and Miller (1963:118) suggested, that the

gamefish stocked in Timpie Springs came from the Pecos River in New Mexico, where *Lucania parva* abounds, and the circumstantial evidence points to the conclusion that a brood stock of *Lucania parva* accompanied the gamefish.

BLUE LAKE, UTAH

December 28, 1961, 10 half-grown to adult specimens (SIO 62-138-27A) taken by spot-poisoning and Aqualung by Phillip R. Sloan in this 16-meter-deep spring pool on the bed of ancient Lake Bonneville 26.2 km due south of Wendover, near the Nevada border of Utah, about 120 km across very dry desert west-southwest of Timpie Springs.

The collector reported the bottom as clayey sand and the temperature, with inversion (indicating high mineral content), as about 26° C at the surface and 29° C at the bottom. The water contained green algae. The collector took a few young bluegills (*Lepomis macrochirus macrochirus*), and saw adults of this sunfish and of largemouth bass.

Stocking records seem to indicate that the gamefish in Blue Lake, as in Timpie Springs, came originally only from the Pecos River in New Mexico, so that there is reason to think that *Lucania* was inadvertently introduced with the gamefish, from the same source. Donald C. Hales of the Utah Department of Fish and Game wrote on March 1, 1963, that bluegills of unrecorded origin were stocked in Blue Lake in 1953 and that he had learned from Marion Madsen that largemouth bass, reportedly stemming from Santa Rosa, New Mexico, were stocked in Blue Lake, as well as in Timpie Springs, in 1947 or 1948.

IRVINE LAKE, SOUTHERN CALIFORNIA

November 5, 1963, 1 subadult (SIO 64-267-27A) seined by James A. St. Amant of the California Department of Fish and Game, along with 2 other specimens that escaped.

June 18, 1964, 6 young (SIO 64-322-27A) seined by Keith W. Radford and party on the west shore about 0.8 km south of the dam (Santiago Dam), among much fine algae, at 33° 46' 43" N. Lat., 117° 43' 34" W. Long. These specimens were the only ones obtained in a full day of seining in an effort to obtain a good series.

Irvine Lake is in the Santa Ana River system, in Orange County. It is a reservoir, fed primarily with Colorado River water, which though high in salts for a water supply is much fresher than most waters inhabited by *Lucania*. The fin rays and vertebrae seem to be weakly ossified, a condition that may have resulted from the relatively low mineral content of the water.

Mosquitofish, *Gambusia affinis affinis*, and fingerling largemouth bass, *Micropterus salmoides salmoides*, abound in this lake. Records of the California Department of Fish and Game (furnished by James A. St. Amant) indicate that the lake was stocked with largemouth bass, bluegills, black

crappies, *Pomoxis nigromaculatus* (Lesueur), bullheads, *Ictalurus* sp., and other gamefishes, all received from fishery stations on the Pecos River, New Mexico: five stockings from Dexter, in 1942, 1943, 1946, and 1948 (2), and one from Roswell, in 1947. The only plausible assumption on the source of the rainwater fish in Irvine Lake is that some were brought in from the Pecos River with one or more of the plantings of gamefish.

SOURCE OF *Lucania* POPULATIONS IN UTAH
AND SOUTHERN CALIFORNIA

Very good reasons support the hypothesis that the establishment of *Lucania parva* in Timpie Springs and Blue Lake, Utah, and in Irvine Lake, southern California, discovered in turn in 1959, 1961, and 1963, is attributable to inadvertent introductions from the Pecos River in New Mexico. As indicated above, each of these three isolated waters has been stocked with gamefish from federal fishery stations on the Pecos in New Mexico. *Lucania parva* abounds in the well mineralized waters of Pecos River (p. 43, Fig. 1), and is a fish that would be expected to flourish in fish ponds.

We have no specific evidence of *Lucania parva* having been included in shipments of gamefish, but on a number of occasions we have observed "sleepers" of other "minnows" in such shipments. Three pertinent examples of such observations may be cited. On November 20, 1948, Willis A. Evans of the California Department of Fish and Game, on checking a sample of several gamefishes from the Dexter station on the Pecos River being stocked in Vail Reservoir, Orange County, California, picked out and submitted to Hubbs specimens of two cyprinodonts, a species of *Cyprinodon* (CAS 20370) endemic in the Pecos River, and *Gambusia affinis affinis* (CAS 20369). Another such observation was the inclusion of at least one *Lucania goodei* (SIO 64-272-27A) in the first shipment to California in 1959 of Florida largemouth bass, *Micropterus salmoides floridanus* (Lesueur), from the Pensacola Fish Hatchery of the Florida Game and Fresh Water Fish Commission. The introduction of a cyprinodont, *Fundulus zebrinus*, and a cyprinid, *Notropis stramineus* (Cope), into Arizona is specifically attributed to "an accidental planting when two shipments of largemouth bass from Dexter, New Mexico, were stocked in 1935" (Miller and Lowe, 1964:142, 146).

We have considered, and now tend to regard as implausible, the alternative hypothesis that *Lucania parva* was incidentally stocked, in some or all of the Western waters in which it has been established, along with mosquitofish (*Gambusia affinis affinis*), which have been very widely spread in mosquito-control operations. We have had no indications of such introduction, although mosquitofish have long become thoroughly established in Utah

(Rees, 1934 and 1945; Sigler and Miller, 1963:120-22), Nevada (Miller and Alcorn, 1945:184), and California (Dill, 1944:162-63, and personal observations). Furthermore, health authorities in these states are maintaining and distributing stocks of mosquitofish presumably free from contamination with other cyprinodonts.

Aquarium fish are now, disconcertingly, becoming established in many waters in the West (see, for example, Deacon, Hubbs, and Zahuranec, 1964), but *Lucania* is all but unknown in the home-aquarium trade. It is extremely unlikely that any of the establishments in the West are explicable in terms of escaped or dumped aquarium specimens.

SOURCE OF THE *Lucania* POPULATIONS IN
SAN FRANCISCO AND YAQUINA BAYS

Although we feel reasonably secure in attributing the introduction of *Lucania parva* into Utah and southern California to the inclusion of this cyprinodont in shipments of gamefishes from federal fishery station (s) on the Pecos River, New Mexico, we do not find evidence that the populations about San Francisco Bay, California, and Yaquina Bay, Oregon, arose in this way. Leo Shapovalov of the California Department of Fish and Game reported (letter of December 17, 1959) that he had "not been able to locate any definite information on shipments of fish into California from the U. S. Fish and Wildlife Service hatchery at Dexter, New Mexico, in relation to the appearance of *Lucania* in the San Francisco Bay area." Carl E. Bond has furnished similar negative indications for the Yaquina Bay area, stating (by letter of January 8, 1959) that "we have no knowledge of any recent legal introductions of any game fish or other fish into the Yaquina River system." The possibilities of its introduction into these waters through its inclusion with *Gambusia* in mosquito-control operations or through the escape of home-aquarium specimens seem even more remote for the bays than for the interior waters.

What appears to us to be a plausible hypothesis on the introduction of the rainwater fish into San Francisco and Yaquina bays is that it was transported as eggs on oysters, *Crassostrea virginica* (Gmelin), from the East Coast of the United States. This idea, which was suggested to us by Jay D. Andrews of the Virginia Fisheries Laboratory (now the Virginia Institute of Marine Science), seems very plausible on two grounds: *Lucania*, according to Andrews (personal communication), is common and spawns on oyster reefs, and eastern oysters have been cultivated extensively in San Francisco and Yaquina bays.

During the last quarter of the nineteenth century enormous quantities of seed oysters, as much as 262 carloads per year, were transported to San Francisco Bay annually, from mid-March to mid-May and from mid-October

to mid-November (Barrett, 1963). In this connection we note that a long spawning season, from early April until near the end of July, was attributed to *L. parva* in Chesapeake Bay by Hildebrand and Schroeder (1928:137). Barrett wrote: "Most of these came from the bays and estuaries of New York and northern New Jersey, principally Newark Bay and the North River, but also the Raritan River, New Jersey, and Prince Bay, Staten Island. . . . Probably 1910 was the last year that eastern seed oysters were imported to San Francisco Bay. . . . Fully-grown eastern oysters continued to be imported however, and many of them were held in beds in San Francisco and Tomales bays until sold."

Production of eastern oysters in California continued through the 1950's, but by the end of the decade became a negligible proportion of the total production, as the giant Pacific oyster, *Crassostrea gigas* (Thunberg) of Japan, took over.

Concerning the introduction of *Crassostrea virginica* into Yaquina Bay, R. E. Dimick reported (by letter of March 15, 1963) as follows:

"There have been a number of east coast oysters planted in the bay from about 1878 to some time in the early 1940's. Information on the first plant occurred in the Daily Oregonian for August 12, 1896, as follows:

Captain J. J. Winant, some 18 years ago while engaged in planting eastern oyster plants in San Francisco Bay, concluded to try the experiment at Yaquina Bay. He brought by sailing vessel two barrels of young Chesapeake bay oysters, there being about 5,000 in a barrel, and placed them near the mouth of Pools Slough which empties into Yaquina Bay. The plants were 8 days crossing the continent to San Francisco and after being placed in the bay for 24 hours, they were brought north being 10 days on the way. It was 19 days from the time the plants left the eastern waters before they were scattered over the bed of Pools Slough. Within 18 months several bushels of oysters, considerably more than half grown were secured. Ten years after this, eastern oysters were taken from the natural beds showing beyond doubt that a few of the oysters had spawned.

"Dr. Nathan Fasten stated in an article on the Yaquina oyster beds (1931, American Naturalist, Vol. LXV:434-68): 'There have also been numerous plantings of the Atlantic oyster, *Ostrea virginica* Gmelin, but with few exceptions these have not acclimated themselves to their new location in the Yaquina region.'

"As Carl Bond told you, we received an experimental plant of seed oysters from Rhode Island sometime in either 1943 or 1944. . . . I suspect that most of the earlier shipments came from Chesapeake Bay. . . . I suspect that the last were shipped when Pacific oysters became available in the bay (about 1940)."

According to the advice of Chester N. Wachsmuth of the Oregon Oyster Co., dated April 22, 1963, and received through R. E. Dimick, the last commercial shipment of seed oysters into Yaquina Bay arrived about 1931; this

20-barrel shipment (much smaller than some earlier shipments) was sent by the Warren Oyster Co. of Rhode Island, which had beds in Narragansett Bay.

The circumstance that eastern oysters probably have not been transported to San Francisco Bay or Yaquina Bay since the 1950's or 1940's, respectively, does militate against the hypothesis, but ichthyological studies along and near the shores of these bays have been limited; furthermore, an introduced animal often builds up its population slowly until it quickly explodes in numbers (witness the well-documented history of the establishment of the sea lamprey, *Petromyzon marinus*, and the smelt, *Osmerus mordax*, in the Great Lakes).

The hypothesis of the introduction of *Lucania* along with oysters is rendered more plausible when we consider the evidence that other marine organisms may have been introduced into western North American waters incidentally by such a pathway. Several such introductions have been hypothesized by Bonnot (1935) and Hanna (1939), who listed numerous Japanese molluscs and one species of barnacle found in a shipment of seed oysters in 1930, before a rigid inspection was established. Two of the best authenticated introductions on oysters are those of two oyster pests, the Atlantic oyster drill, *Urosalpinx cinerea* (Say), which obviously arrived with spat of the Atlantic oyster, and the Japanese oyster drill, *U. japonica* (Dunker), which obviously arrived with spat of the giant Pacific oyster (Barrett, 1963:19). The establishment of the channeled whelk, *Busycotypus canaliculatus* (Linnaeus), in San Francisco Bay as early as 1948 (possibly 1938) appears to us, on the basis of Stohler's statements (1962), to be most plausibly explained as owing to introduction with Atlantic oysters. The fortuitous distribution of barnacles, including the introduction of *Balanus amphitrite hawaiiensis* Broch into California, seems thus explicable (Utinomi, 1960). It is thought that the Japanese littleneck clam, *Tapes semidecussata* Reeve, may have arrived in that way (Fitch, 1953:67). It is being theorized (Carl L. Hubbs and John H. Prescott, MS) that an Asiatic goby, *Tridentiger trignocephalus* (Gill), in egg stages reached San Francisco Bay on the giant Pacific oyster, and Los Angeles Harbor among fouling organisms on a ship. The Oriental shrimp, *Palaemon macrodactylus*, which has become established in waters about San Francisco Bay and occurs in association with *Lucania parva*, may have arrived in the same way, though transportation in ship's sea-water system has been hypothesized as more plausible (Newman, 1963). An estuarine Japanese goby, *Acanthogobius flavimanus* (Temminck and Schlegel), may have arrived in the same way as the shrimp (Brittan, Albrecht, and Hopkirk, 1963). The flourishing establishment of the northern Japanese alga, *Sargassum muticum* (Yendo), along the Pacific coast from Oregon to British

Columbia is definitely attributed to transfer on seed oysters (Scagel, 1956; 1957:123). Quayle (1964) presented a detailed study of the introduction and establishment in British Columbia waters of various pelecypod and gastropod molluscs, "largely as a result of oyster cultural operations." The same subject had been treated previously by Carl and Guiguet (1958).

Another plausible hypothesis that may explain the recent introduction of *Lucania* into Yaquina Bay (and presumably applicable also to San Francisco Bay) is that the fish have been introduced in water ballast. Through W. P. Breese of Oregon State University we learned in 1963 that Mr. Wade of the Yaquina Dock and Dredge Co. has made this suggestion, which the chief engineer for the Calmar Lines thinks is entirely possible, adding that, for example, about 3 years previously, because of the steel shortage, ships came from the East with ballast (from the Chesapeake area) and pumped it out in Yaquina Bay; this could also have occurred earlier when cargo for the West was unavailable. This hypothesis fits better the indications that *Lucania* is a recent introduction.

While this paper was in press, evidence has come to our attention of the establishment, probably temporary, of another Atlantic coast cyprinodont, *Cyprinodon variegatus* Lacépède, in an estuary near the mouth of Dungeness River, on the Olympic Peninsula of Washington. Greenfield and Grinols (1965) in reporting the capture of 28 specimens there in 1949 discussed historical evidence bearing on the possibility that the species was introduced with oysters from the Atlantic coast. They concluded that the introduction resulted "directly from a discarded aquarium [which seems to us unlikely], or indirectly from an unofficial transplantation of eastern fish or shellfish species." We are informed that there is an oyster farm in adjacent waters (David W. Greenfield, personal communication).

MERISTIC AND MORPHOMETRIC EVIDENCE ON THE ORIGIN OF THE WESTERN POPULATIONS

A comparison of the meristic and morphometric data for the five introduced populations of the western United States with the data for the naturally occurring populations from southern New England to north-eastern México has a double bearing: resemblances between a given introduced population and the ancestral stock hypothesized on circumstantial evidence strengthen the hypothesis; differences suggest phenotypic modifications attributable to changed environment. Such resemblances and differences are considered together in the following analysis. The San Francisco and Yaquina bay populations are considered as one unit because of certain similarities in character as well as in habitat, and because it is hypothesized that they both arrived on shipments of oysters or in water ballast from the North Atlantic coast. The interior populations, from

Timpie Springs and Blue Lake in Utah and from Irvine Lake in California, are also treated together, largely because circumstances indicate that they arrived with plantings of gamefish from the Pecos River in New Mexico.

The dorsal rays, and more particularly the anal rays (Tables 2, 4, 5; Figs. 2, 3), average lower in the bay and interior-western stocks than in all but a few native populations. The western stocks agree well with the samples from Chesapeake Bay, and with the Pecos collections, and with a few scattered samples from Florida to the Río Grande. An outstanding point, probably attributable to a phenotypic effect, is the low anal counts for the Yaquina Bay and Irvine Lake samples, with a possible slight reduction also in the dorsal counts for Yaquina Bay. The reduction in the anal counts for the Irvine Lake sample involves both unbranched and branched rays (Table 5).

The principal caudal rays (Table 7, Fig. 4) average uniformly high in count in the western series, agreeing best with the far-northern and Pecos samples, and with a few others. A particularly surprising circumstance is that the one Irvine Lake specimen that was countable, though still small (standard length 20 mm), clearly has the extreme high count of 18 caudal rays, as in only 8 specimens among the other 370 enumerated. An unexplainable phenotypic effect may be indicated.

The pectoral-ray counts (Table 8, Fig. 4) show little of significance, but do not negate the hypotheses on the origin of the western populations. The probable though hardly trustworthy indication of a slight average reduction in Yaquina Bay recalls the reduction in anal-ray count there.

The average number of lateral scale rows and vertebrae (Tables 11 and 15, Fig. 6) is moderately high and rather uniform in the western populations, but is hardly distinctive (except in contrast with certain stocks in Florida). Neither the interior nor the bay samples exhibit the slightly reduced average number of scale rows characteristic of the Pecos River samples. Phenotypic modification seems to be involved.

Even more striking is the circumstance that the interior stocks in the West do not agree with the Pecos River fish in the low averages of transverse scale counts (Tables 12–14)—dorsal-to-anal, around the body (Fig. 5), and especially around the caudal peduncle. The marked tendency toward emaciation in the Pecos, perhaps related to its high content of gypsum, may be involved, in view of the general tendency for the number of scales (and of other meristic elements) to be governed by the absolute space available during the development of the part involved (Hubbs, 1927:82–84; 1941b: 235–36). Again a phenotypic effect seems to be involved. In these three scale counts the bay forms of the West seem to average higher than the interior forms, which circumstance somewhat strengthens the idea that the bay forms

stemmed from the far north, where the averages are high, and that the interior forms stemmed from the Pecos.

In respect to the counts of preopercular and supraorbital pores (Tables 16–17, Fig. 7) we find perhaps the strongest evidence that the stocks of the western bays came from the far north, and that the interior stocks came from the Pecos. The very high variability in the numbers of these pores points toward either the far north or the Pecos for each set of pores, and the degree of variation points toward the hypothesized origin of each category. The greater variation for the Yaquina Bay samples as compared with those for San Francisco Bay may reflect the circumstance that in general it was necessary to utilize smaller specimens from the Yaquina Bay area (as noted above, pore formation tends to be completed late in life). However, some difference in origin of stock or some phenotypic differential may be involved.

The lachrymal pores (Table 18, Fig. 7) tend to average few, with complete lack frequent, in the western bays as in the far north. The more frequent reduction in Yaquina Bay again may largely reflect the unavoidable reliance on smaller adults. Similarly, the tendency toward more complete development in Timpie Springs, as compared with the Pecos, may reflect the exuberance of the spring stock (many large fish were available in each set).

In respect to the mandibular pores (Table 19, Fig. 7) the San Francisco stock agrees with that of the far north (or the Pecos) in the great preponderance of mandibles without any pores. The resemblance, however, is far from exclusive. The almost invariable absence of these pores in the Yaquina Bay specimens may well reflect their small size. Again, the development of the pores is more complete in Timpie Springs than in the Pecos.

In the search for evidence regarding the origin of the western stocks of *Lucania parva* the number of gill rakers (Table 20, Fig. 5) appears to be especially significant. The numbers in the two bay stocks exceed those of any of the native groups except for Long Island and southern New England, which are even more extreme in this respect (the Chesapeake Bay samples are distinctly less extreme). The lower average number in the interior stocks corresponds much better with the value for the Pecos samples, but is not certainly different from the averages of a number of samples from the Gulf of Mexico.

The data on the length of the pelvic fin (Table 21) scarcely contribute to the evidence on the origin of the western stocks, but, on the contrary, indicate the phenotypic basis of the sexual dimorphism, which leads to greatly enlarged pelvics in the males of certain stocks. That this dimorphism is extreme in the Timpie Springs collections, and only slightly evident in its presumed ancestral stock, from Pecos River, has already been stressed (p. 33)

as evidence of the phenotypic exuberance of *Lucania* in the obviously very favorable environment of these springs.

The body depth (Table 22) of the western stocks is about average for the species, and is about uniform. The higher ratios (slenderer body) of the Blue Lake and Irvine Lake series is attributable to the small size of the available specimens.

The anal-to-caudal measurements (Table 24) offer almost nothing of value, and nothing new of importance is provided by the detailed data (Table 25) on proportional measurements.

It is concluded that the evidence of differential characters bolsters the hypothesis that the establishment of *Lucania parva* in Timpie Springs and Blue Lake, Utah, and Irvine Lake, California, is attributable to fortuitous introduction with gamefish from federal fish-culture station(s) on the Pecos River, in New Mexico, and that the occurrence of the species in waters about San Francisco and Yaquina bays resulted from fortuitous introductions with oysters from the North Atlantic Coast of the United States, from some point between New York and Chesapeake Bay.

Lucania interioris,² new species

(Figs. 1-8, Pl. III)

The discovery of this isolated endemic species of an interior-drainage basin far inland in northeastern México is briefly recounted above (p. 5). Its habitat and its distributional relations are detailed below. Its occurrence in an interior basin is consonant with the already mentioned broad ecological tolerance of its wide-spread close relative *Lucania parva* (p. 12).

RELATIONSHIPS

The relationships of this species are clearly shown by its morphological characters and are reflected in its habitat and behavior. Many features affirm its pertinence to the family Cyprinodontidae, tribe Fundulini, and genus and subgenus *Lucania*. It is obviously oviparous, for large eggs fill its single, slightly bilobed ovary; the anal fin of the male and its suspensorium are scarcely modified and the branching of the anal rays and the neuromast pattern are typical of the family (Hubbs, 1950:7-8). Pertinence to the tribe Fundulini, as diagnosed by Myers (1931:249-50), is indicated by the fully protractile premaxillaries, relatively low pectorals, toothless vomer, and absence of pseudobranchiae. Its free orbital border contrasts with that of *Rivulus* and its relatives though it agrees with those genera in having a rather narrow lachrymal ("preorbital"), which is only 0.3 as wide as the eye, as in *Lucania parva* and some other Fundulini

² The name *interioris*, "dwelling in the interior," seems particularly appropriate.

(Myers' statement that the preorbital in this tribe is half eye or more is not always strictly true).

L. interioris agrees in many respects with the two other species we accept as comprising the genus *Lucania*, in contrast with *Leptolucania* (Table 1). The only apparent approach to *Leptolucania* is the relatively slight backward shift in the position of the dorsal fin. Several of the characters compared in Table 1 testify to a close relation with *L. parva* rather than with *L. goodei*. The close genetic tie of *L. interioris* with *L. parva* is particularly well shown by common and distinctive features of coloration, as can readily be appreciated by comparing the illustrations of *L. parva* (Pls. I-II) and *L. interioris* (Fig. 8) in this treatise and those of *L. parva* and *L. goodei* in the paper by Hubbs, Walker, and Johnson (1943:9-14, pls. 4-6). Especially striking and significant is the agreement between *interioris* and *parva* in the sexual dimorphism in pigmentation—the lower half of the front edge of the dorsal fin in the mature males (and to a lesser extent in developing males) of each species is jet black, set off behind and below by a light area.

COMPARISON WITH *Lucania parva*

The characters that differentiate *L. interioris* on the specific level from *L. parva* are detailed in Table 27 (and in the tables therein referred to). The data on *L. interioris* presented in Tables 1 and 27 constitute a firm diagnosis of the species. Though subject to sexual dimorphism (see especially page 33), the first character entered in Table 27 suffices alone to separate all individuals of *interioris* from all of *parva*, irrespective of sex; the ratio that gives expression both to the shorter pelvic fin and the longer predorsal length of *interioris* ranges in large series of each species from 4.9 to 6.5 in *interioris* and from 2.5 to 4.8 in *parva*.

In the feature just mentioned and in some other respects the two species are completely differentiated morphologically. Although no grounds whatever appear for questioning its pertinence to the genus and subgenus *Lucania*, we feel that the evidence calls for according *L. interioris* full species rank. There seems to be no chance of intergradation in nature between this species and *L. parva*, because, as noted below, extensive collecting in the Río Salado system has indicated that no form of *Lucania* occurs there.

The only other stock of *Lucania* that lives so far inland, and the one that occurs nearest to the Cuatro Ciénegas Basin, namely that of the Pecos River (p. 43), is so little modified from the coastal forms of *L. parva* as to be inseparable even on the subspecies level. Neither this Pecos race nor those of interior Florida approach *L. interioris* significantly.

In the very weak development of cephalic sensory pores this form

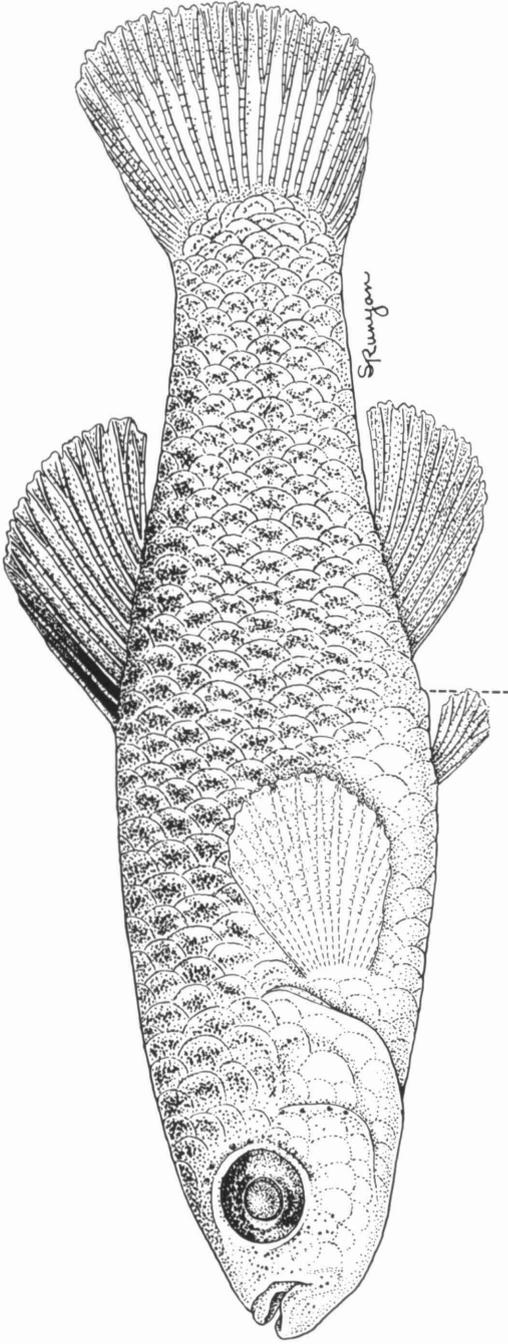


FIG. 8. Holotype of *Lucania interioris* (UMMZ 179850).
An adult male 26.5 mm in standard length, from La Angostura Canal, 2.56 km south
of Cuatro Ciénegas, Coahuila, México. Drawn by Suzanne Runyan.

approaches or resembles far-northern populations of *L. parva*. This resemblance suggests the possibility that *L. interioris* may be a Pleistocene relict that originated when the entire range of *L. parva* was shifted southward. Alternative explanations, however, seem at least equally plausible. One hypothesis is that this local endemic of reduced size may retain juvenile characters (the pore pattern is completed relatively late in development). In some other respects, as in the position of the anus (reflected in the predorsal length and urosome length), *L. interioris* essentially resembles the southern New England stock of *L. parva*.

DESCRIPTION

Like many forms of isolated spring waters (Hubbs, 1941a), *L. interioris* is distinguished by its small size (its maximum standard length is 31 mm), more posteriorly inserted dorsal and anal fins, generally deeper caudal peduncle in proportion to the body depth, usually longer and typically wider head and interorbital, and generally smaller and more rounded dorsal and anal fins (Table 25). The smaller size of the pelvic fins and their occasional absence in *L. interioris* illustrates the tendency for the pelvic fins to degenerate in desert-spring cyprinodonts (Hubbs, 1932b:2; 1940:201; Miller, 1948). The inner edges of the pelvics are united to the body, and more or less to one another, for one-fourth to three-fourths of the length of these fins (probably to a greater extent than is usual in *L. parva*).

In most meristic and morphometric characters not mentioned in Table 27, *L. interioris* agrees with *L. parva*, or the counts or proportions overlap too widely to be of diagnostic value. The meristic data are presented in Tables 2–20, several morphometric ratios are given in Tables 21–24, and proportional measurements are detailed in Table 25. Some of the data are analyzed graphically in Figures 2 and 4–7.

The gape is strongly angulated, and the upper-anterior part of the mouth is subhorizontal, while the preorbital edge, in an even curve, slopes slightly backward as well as downward posteriorly. The teeth, as in *Lucania parva*, are few, large, slightly flattened, and pointed.

In *L. interioris*, as in *L. parva* (see Hubbs, Walker, and Johnson, 1943:9–14, pls. 4–6), all scale pockets except on the breast and the middle of the belly are conspicuously and regularly outlined with dark streaks.

COLORS IN LIFE.—Colors were first recorded in the field, in direct sunlight, for an adult male and an adult female briefly held in a small aquarium; later taken from a Kodachrome of a live nuptial male kept by W. L. Minckley and from notes recorded by him for several nuptial males in his laboratory in Kentucky. In the male, the dorsal fin is a conspicuous chalky-blue, which color becomes intensified on the anal fin, where it varies from turquoise to deep blue except on the narrow dusky to black margin; the blotch on the

first 2 interradiation membranes of the dorsal is velvet-black; the caudal fin is dusker, with a darker base and margin, and with only a wash of pale bluish to bluish green; the pectoral varies from weak to intense orange, becoming reddish orange basally and abruptly black along the distal margin; the pelvic is orange, with black toward the distal margin. The body is marked by horizontal rows of chalky blue spots that cover the centers of the scales comprising at least 7 rows on the sides; in extremely high males these spots become turquoise. Intervening between these rows are borders and horizontal lines of olive to orange (depending on the breeding condition; becoming a more intense orange as breeding behavior attains maximum expression). The general body color is bronze to golden. The back from the occiput to below the entire dorsal fin is olive-green, blotched darker and lighter. Blue glints are reflected from the blotch behind the eye and from the opercular region. The lower part of the head and the preopercular region are orange-brown; the top of the head is dusky olive. A blackish bar crosses the lower part of the eye. The female is generally pale brown, with no bright colors.

NUPTIAL TUBERCLES.—On adult males collected in April, 1961, the tubercles on the scales are arranged as in *Lucania parva*—on the top and sides of the head, on the sides of the body (chiefly posterior to the dorsal origin), and on the rays of the dorsal and anal fins. These structures had become largely resorbed in males taken in mid-August, 1960. On the top of the head tubercles line the entire margin of the large, nonimbricated scale, which lies between the orbits, and also line the free edges of the other scales, from the rostrum to above the vertical arm of the preopercle. A few tubercles are scattered over the sides of the head, mostly above the level of the ventral edge of the base of the pectoral fin and behind the eye; a few may occur below the eye, but not anterior to it. From 1 to 9 tubercles line the margin of each scale along the rows on the sides of the body, from the third row above the origin of the anal fin to the second full row below the origin of the dorsal fin; these contact organs are developed forward to above the insertion of the pelvic fins and posteriorly to the caudal base. Similar organs are distributed along the outer halves of the dorsal and anal fins from about the second anal and third dorsal ray posteriorly.

BREEDING BEHAVIOR

As determined by Neal R. Foster, who is conducting a detailed comparative study of the breeding behavior of cyprinodontids, *L. interioris* displays some distinctive breeding-behavioral traits (personal communication). Just prior to the spawning clasp, the male of this species contacts the female's venter with the top of his head, as do the males of *L. parva* and *L. goodei*,

but, unlike those species, *L. interioris* spawns against fibrous substrata at or near the bottom (a trait also observed by W. L. Minckley). *L. goodei* and *L. parva* almost invariably spawn close to the surface, even when fibrous substrata are absent there. All three forms court close to the bottom. Foster suggests that the distinctive spawning-site preference in the new species may be a behavioral adaptation either to the absence of suitable spawning sites near the surface or to the intense solar radiation of the region (or, we might add, to the extremely shallow waters of the normal, native habitat). A further possibility suggested by Foster is that the spawning-site preference may be a primitive behavioral trait.

TYPES

All known material of *L. interioris* has come from within the Cuatro Ciénegas Basin, in central Coahuila, México. The holotype (UMMZ 179850), an adult male 26.5 mm in standard length, was collected in La Angostura Canal 2.56 km by dirt road south of Cuatro Ciénegas (Fig. 1, Loc. 3 on insert) on April 8, 1961, by Robert R. Miller and family, Carl L. Hubbs, and W. L. Minckley. Taken with the holotype were 6 male and 2 female paratopotypes (UMMZ 179851; 18.0–24.0 mm). The following paratypes were obtained: 3 adult males and 5 adult females (UMMZ 179840; 23.0–31.0 mm), from Ferriño's Canal (Fig. 1, Loc. 7), about 2.4 km by road south of San Juan (at east end of basin), collected on April 7, 1961, by Miller, Hubbs, Minckley, and José Lugo, Jr.; 114, juvenile to adult (UMMZ 179853; 11.0–27.4 mm), from a marshy pool (Pl. III) along the eastern edge of Río Garabatal (near source of La Angostura Canal) approximately 8 km west-northwest of the tip of San Marcos Mountain (Fig. 1, Loc. 1), taken on April 8, 1961, by the same collectors; 5 juvenile to adult (UMMZ 179189; 17.0–25.0 mm), from the small stream discharging from Los Positos, 4.8 km south and 8.3 km east of Cuatro Ciénegas (Fig. 1, Loc. 5), collected on August 18, 1960, by Minckley and James E. Craddock; 2, immature (UMMZ 179182; 14.0–15.9 mm), from La Angostura Canal at same station (Loc. 3) as holotype, taken on August 18, 1960, by Minckley and Craddock; 2, adult females (UMMZ 130389–90; 23.5–26.0 mm), from an unspecified locality near Cuatro Ciénegas, collected August 28, 1939, by E. G. Marsh, Jr.; 8, half-grown to adult, 1 male and 7 females (UMMZ 130379, 15.0–25.0 mm), also from an unspecified place near the same village, collected on August 15 by Marsh; the probable locations of Marsh's collections (which are not spotted on the insert in Figure 1) are discussed below (pp. 64–65).

Subsequent to the collection and designation of the types, W. L. Minckley (personal communication) and associates have collected the following series of *L. interioris*:

Marshy pools along eastern edge of Río Garabatal, at same locality (Fig. 1, Loc. 1) fished April 8, 1961; collected April 18, 1963, by W. L. and Barbara Minckley and Richard K. Koehn (KU 7433, 80 specimens, and INIBP, 5 specimens).

La Angostura Canal, about 8 km southwest of Cuatro Ciénegas village (Fig. 1, Loc. 2); taken April 15, 1963, by same collectors (1 adult removed from series of *Cyprinodon* sp.).

La Angostura Canal, 2.56 km south and 1.6 km east of the village (Fig. 1, Loc. 4); taken April 19, 1963, by same collectors (KU 7437, 1 specimen).

Ferriño's Laguna, 11.2 km east and 3.2 km south of the village (Fig. 1, Loc. 6); taken June 9, 1964, by W. L. Minckley and party (ASU 64-0953, 22 specimens, largely adult, examined by senior author September 13, 1964).

Two additional specimens (ASU 64-0758) were aquarium reared from stock collected in April, 1961.

"Ditches just east of village of Cuatro Ciénegas" (presumably southeast, as there are no ditches directly east); collected April 2, 1963, by David A. Etnier (UMinn; more than 20 specimens). Information from collector through W. L. Minckley. Location too uncertain to spot on the insert in Figure 1.

HABITAT AND ASSOCIATED FISHES

The features of the habitat where specimens were collected, as recorded in the field notes for 1960 and especially for 1961, were as follows. The water, though very clear, was readily muddied because the bottom was of deep mud to fine detritus and firm clay (with some sandy silt and gravel). The water at all stations was at least slightly saline; in places, highly alkaline. In the artificial canals (La Angostura and Ferriño's) the depth was generally only 15 to 23 cm, at most 45 cm; in the marshy pool (Pl. III) the depth was less than 15 cm; in the outflow from Los Positos the depth was about 45 cm. Aquatic vegetation consisted chiefly of an abundance of *Chara*, with *Juncus*, salt grass, and tules at the margins. The immediate shore was a mesquite border and desert flat at the canal stations and banks of crystallized salt at Los Positos; marshy sedge meadows (Pl. III) surrounded the most favorable habitat. Water temperatures varied from 17° to 27° C in early April, 1961, when the air fluctuated from 18° to 32° C at the same stations. The current varied from moderate, with an estimated flow of 0.6 to 0.9 m³/sec, to none. The canals varied from 1.0 to 2.5 m wide, and the marshy pool (Pl. III) was about 4.5 × 6.0 m in major dimensions. All habitats were almost completely free of shade. In the marshy pool, the species when disturbed dove into the thick, flocculent mud bottom (in capturing the series of 114 individuals we repeatedly and vigorously stirred the bottom with feet and brails as we advanced slowly with a well-leaded 4.7-m "Common Sense" seine).

Changes in the habitat of *L. interioris* may be severe. The marsh-pool habitat worked April 8, 1961, was in similar condition on April 18, 1963 (W. L. Minckley, personal communication), with the highly saline water about 20 cm deep, but somewhat encroached by vegetation. On June 7, 1964,

these highly saline pools were only about 5 cm deep and very warm (41.5° C); no *Lucania* remained and other fishes were killed by toxic compounds released when the deep silt bottom was churned up.

Conditions were somewhat different in Ferriño's Laguna, worked by W. L. Minckley on June 9, 1964. The shallow, 4-hectare depression of the marshy lagoon was crossed by drainage ditches. The soft bottom showed salty deposits. The water, at most about 75 cm deep, was covered with *Chara* and, in places, *Distichlis*. The margin was a salt-grass flat with some sedges.

In the canals, *L. interioris* was associated with an abundance of two other cyprinodonts (an undescribed form of *Cyprinodon* and *Gambusia marshi* Minckley and Craddock, in Minckley, 1962) and with smaller numbers of *Astyanax fasciatus mexicanus* (Filippi) and *Cichlasoma* cf. *cyanoguttatum* (Baird and Girard). In the marshy pool it was taken with the same forms of *Cyprinodon* and *Gambusia*, and with *Gambusia longispinis* Minckley (1962); in 1963 the *Cichlasoma* also occurred here. At Los Positos it was seined with *Gambusia marshi*, with the forms of *Astyanax* and *Cichlasoma* named above, with another form of *Cyprinodon*, and with a subspecies of *Dionda episcopa* Girard, and with *Ictalurus lupus* (Girard) and *Micropterus salmoides*. At Ferriño's Laguna the associated fishes were *Dionda episcopa* subsp., *Cyprinodon* sp., and *Gambusia marshi* and *longispinis*.

DISTRIBUTIONAL RELATIONS

The discovery about 30 years ago of *Lucania interioris* and of other endemic species in the interior basin of Cuatro Ciénegas (Fig. 1, insert, Pl. III), in the state of Coahuila, northeastern México, is briefly recounted in the Introduction (p. 5). This basin, arid except for the marshes and irrigated fields, until recently comprised two major sections, one of which, apparently comprising the entire range of *L. interioris* and most of the basin, was of interior drainage, containing numerous springs, streams, and pools on the surface and within the limestone substrate. The other section of the basin, along its southeastern and eastern margin, drained eastward through two successive water gaps into the Río Salado de los Nadadores, a tributary of Río Salado, in the drainage basin of the Río Grande. In recent years the flat sill on the east side of the enclosed basin has been deeply entrenched by a large drainage ditch, through which the waters of the formerly enclosed section now discharge into the exterior drainage. Brief accounts of the basin have been given by Gilmore (1947), by Taylor (1956), and, most pertinently, by Webb, Minckley, and Craddock (1963).

There is evidence, albeit indirect, that Cuatro Ciénegas Basin has long been isolated and has long contained surface water. An examination of the exposed alluvium along the sides of the deep trench of the artificial outlet

ditch, in 1961, suggested to the senior author that the deep alluvial sill represents a massive bajada fill attributable to pluvial erosion from the mountains to the north. Pleistocene dating of the sill is suggested, along one line of evidence, by failure to find any signs of human occupation in the walls of the deep trench, or of adjacent washes in the sill area, except in the most superficial layers. There is good evidence, certainly in line with reasonable expectation, that man occupied this favorable basin throughout Recent time—a broad spectrum of radiocarbon dates, based on wood fragments and organic artifacts from an excavation of Frightful Cave along the eastern margin of the basin (Taylor, 1956), range from 9540 to 1770 B. P. (before present). In a report on the mammalian remains that Taylor obtained in 1940–41 in the archeological sites of this and other caves around the basin, Gilmore (1947) concluded from the faunal evidence that the basin during the time when the mammals were captured was moister than at present. Because the older radiocarbon dates for the basin approximate what now appears to have been the close of the Pluvial period, and because the Mexican Plateau was definitely included in the area of Pluvial regime, it may be concluded that conditions suitable for fish life have probably existed within the basin for tens of thousands of years, during much of which time a considerable part of the area was probably of interior drainage. At least moderate antiquity has just been indicated for Ojo de la Becerra, one of the main spring-fed pools of the enclosed section of the Cuatro Ciénegas Basin. Peat from a depth of 2.25–2.35 meters in a core in the bottom of this pool has yielded a radiocarbon date of $2,070 \pm 250$ B.P., regarded by Paul S. Martin, who collected and submitted the sample, as a roughly median date for this spring pool (LJ-992, being reported by Hubbs, Bien, and Suess, 1965).

It seems almost certain that *Lucania interioris* is properly interpreted as an isolated endemic. Intensive collecting through northeastern México for more than 30 years has failed to locate it beyond the confines of Cuatro Ciénegas Basin. Particularly extensive recent collecting in the Río Salado system, such as that which led to the discovery at many stations of the endemic shiner *Notropis saladonis* Hubbs and Hubbs (1958), has indicated with considerable assurance that neither this species nor any other form of *Lucania* occurs in this river system below the Cuatro Ciénegas Basin. The circumstance that *L. interioris* shares some characters with the northernmost form of *L. parva* suggests that it may be a Glacial relict. The genus may have been much more widely spread in México during Quaternary periods of greater rainfall. Whether the species *interioris* is autochthonous in the Cuatro Ciénegas Basin or merely relict there is undeterminable.

Within the western part of the enclosed section of the Cuatro Ciénegas Basin there appear to have been, prior to the recent ditching, at least four

small stream flows, locally known as: (1) Río Garabatal, in the northwest; (2) Río Mesquites, the largest stream, flowing north to the west of Sierra de San Marcos, then eastward; (3) a separate flow at Río Puente Chiquito, north of Río Mesquites and south of Cuatro Ciénegas; and (4) another small flow at Río Puente Colorado, on the opposite (south) side of and tributary through a marsh to Río Mesquites (Webb, Minckley, and Craddock, 1963, especially map, fig. 3). Farther east, and probably also to the southeast, there appear to have been a considerable number of more or less completely separate marshes and limestone spring pools. The two main drainages (of Río Garabatal and the Río Mesquites complex) appear to have maintained some faunal distinctions, including differentiation within species. *Lucania interioris*, despite its essential integrity, seems to partake of such differentiation, at a racial level.

The waters inhabited by *L. interioris* appear to include two or more originally separate subdivisions of the Cuatro Ciénegas Basin (see insert on Fig. 1). One of these definitely is that of Río Garabatal and associated marsh waters, which now form the source of an irrigation ditch known as La Angostura Canal. It is therefore plausible to assume that the series from a marsh pool adjacent to Río Garabatal (Loc. 1 on the map insert) and the set from La Angostura Canal (Loc. 3) are parts of the same stock.

The Los Positos (Loc. 5) and Ferriño's Canal (Loc. 7) series may also have had some recent or remote connection. Los Positos are limestone-spring pools in close proximity to a canal that is artificially fed by waters from the Río Mesquites system and empties into the deep ditch that now drains all but the southeastern and eastern margins of the whole basin (however, the outflow from Los Positos, wherein the *Lucania* sample was taken, is not known to connect with the ditch); Ferriño's Canal, though sampled about 8 km east of Los Positos, originates in pools or marsh only about 2.4 km across the flat basin from those pools. Los Positos and the presumably nearby original habitat in the Ferriño's Canal drainage may now have, or may have originally had, an underground connection in limestone channels, or even a surface connection in time of flood.

Unfortunately it has not been possible to determine the precise location of the two collections where E. G. Marsh, Jr. first collected the species. His field notes for the basin were accidentally lost in the field, his labels carry no detailed location, and, when recently consulted, he could not recall details. However, the collections came from the basin south of the village of Cuatro Ciénegas, and the locations spotted by him on a locally undetailed map of the state of Coahuila indicate the probability that one collection (XV) came from the vicinity of Río Mesquites and that the other set (XVI) came from near what is now known as Río Puente Chiquito, which issues from a large limestone spring (this spring terminates what may be a

northern subterranean tributary of Río Mesquites). However, recent collections in those areas have failed to confirm the presence of *Lucania*, and the specimens may have come from marshes or pools nearer the village, in the vicinity of La Angostura Canal. Marsh's collections, therefore, may or may not represent yet another separate section of the interior drainage of the Cuatro Ciénegas Basin.

DIFFERENTIATION WITHIN *Lucania interioris*

In several respects the La Angostura Canal and the Río Garabatal series, which, as expected, agree with one another, differ from the Ferriño's Canal and Los Positos series, which in general are much alike. Marsh's samples in several but not in all respects are like the La Angostura-Garabatal grouping. Unfortunately, the only adequate sample studied is from the pool beside Río Garabatal. The fact that few specimens are included in the Los Positos and Ferriño's Canal series is particularly disturbing. A more thorough study of this species, as indeed of all other fishes inhabiting this unique basin, is much in order.

There are considerable differences in the pattern of variation. The series from the two canals, though different in several respects, are alike in having most often 10 rather than 11 dorsal rays (Table 2, Fig. 2); this may be a phenotypic effect. A similar relation is doubtfully true of the number of anal rays (Table 4, Fig. 2). The unbranched rays in both fins usually number 1 in Ferriño's Canal, but 2 in the other samples (Tables 3 and 5). In the graphical analysis of the regression of anal-ray number on dorsal-ray number (Fig. 3) there appear to be two different, though parallel and steep regression lines: one, to the left in the figure, for the Ferriño's Canal, Los Positos, and Marsh's series; the other, for the La Angostura Canal and Río Garabatal series. The caudal rays (Table 7, Fig. 4) average more in the Ferriño's Canal and Los Positos samples than in the others. The pectoral-ray counts (Table 8, Fig. 4) show little difference. The lateral scale rows (Table 11) average low and the scales around the caudal peduncle (Table 14) average high in the La Angostura Canal and Río Garabatal series, as also in Marsh's material; the other scale counts (Tables 12-13) show no definite patterns. The vertebral numbers (Table 15) average high in the Ferriño's Canal and Los Positos series. The preopercular pores and the supraorbital pores (Tables 16-17, Fig. 7) are typically much more numerous in the Ferriño's Canal and Los Positos series than in the other three; the difference nicely parallels that shown by *Lucania parva* in different parts of its much wider range. The Los Positos series is the only one that shows any lachrymal pores; no specimen of any series has any mandibular pores (Tables 18-19, Fig. 7). The gill rakers (Table 20, Fig. 5)

possibly average more in the Ferriño's Canal series than in the others. The morphometric data (Tables 21-25) seem to show no significant patterns.

SUMMARY AND GENERAL CONCLUSIONS

Lucania is interpreted as including 3 species: (1) the variable *L. parva*, ranging along the continental coast from the southern shore of Cape Cod, Massachusetts, to the lower part of the Río Pánuco system, northeastern México, with interior populations in Florida and in the Pecos River, New Mexico; (2) *L. interioris*, a new, closely related species confined to the nearly enclosed and largely interior-drainage Cuatro Ciénegas Basin in Coahuila, México (this species appears to be slightly differentiated in separate parts of this basin, which is notable for high incidence of endemism among gastropods, fishes, and other organisms); and (3) *L. goodei*, which has commonly been segregated in a distinct genus, *Chriopeops*. Other species previously referred to *Lucania* (or to its generic synonym *Chriopeops*), notably the very distinctive *Leptolucania ommata*, are regarded as not congeneric. *Chriopeops* is recognized as a subgenus.

The meristic and morphometric variations of *L. parva* are in part clinal, in part irregular. This species, like some other estuarine fishes, is particularly modified toward the north end of its range, where its cephalic pores are degenerate but its gill rakers are most numerous. Local differentiation is most intense, and has a largely ecologic relation, near the center of its range, in Florida, where the pale, deep-bodied, few-rayed form of the Florida Keys, with scales in lateral series and vertebrae reduced in number, contrasts with the dark-blotched, slender, many-rayed form of interior fresh waters, with higher lateral-scale and vertebral numbers. Each extreme type is more divergent than any local form of *L. parva* elsewhere, but a connectant series counterindicates recognition of subspecies.

The slightly differentiated Pecos River form approaches neither the interior-Florida stocks nor *L. interioris*.

Consonant with findings for other fishes, numbers of dorsal and anal rays are correlated positively not only throughout the range of *L. parva*, but also within localities. Caudal-ray number, as in other cyprinodonts, is unusually variable. Asymmetrical pectoral-ray counts may tend to be higher in the right fin. One fish has two pelvic fins on one side.

Very recently *L. parva* has appeared in five locations in western United States: San Francisco Bay, California; Yaquina Bay, Oregon; Timpie Springs and Blue Lake, Utah; and Irvine Lake, California. Circumstantial evidence, strengthened by meristic and morphometric analysis (though some features seem to have been altered phenotypically), indicates the probability that the original stocks in the San Francisco and Yaquina bay regions arrived with live oysters or with ballast from the North Atlantic Coast, but that those

in Timpie Springs and Blue Lake, and Irvine Lake, were imported in shipments of gamefish from a federal fish-cultural station on Pecos River, New Mexico.

TABLE I
COMPARISON BETWEEN THE SPECIES REFERRED TO *Lucania* AND *Leptolucania*
Lucania parva and *L. intertioris* are further compared in Table 27

Character	<i>Lucania (Lucania) parva</i>	<i>Lucania (Lucania) intertioris</i>	<i>Lucania (Chriotopeops) goodiei</i>	<i>Leptolucania ommata</i>
Branchiostegals	5 or 6 (usually 6)	5 or 6	5 or 6	3
Postcleithrum	Present	Present	Present	Absent
Oviducal pouch of adult females ¹	Membranous	Membranous	Membranous	Replaced by a pair of specialized scales
Contact organs on top of head of nuptial males	Well developed	Well developed	Well developed	Absent
Premaxillary teeth	Uniserial or irregular; inner teeth, if present, few and strong	Uniserial	Biserial; strong in outer row, weak in inner row	Multiserial; inner rows irregular
Mandibular teeth	Uniserial	Uniserial	Biserial; strong in outer row, weak in inner row	Biserial; strong in both rows
Slope of mouth	Oblique; angle of chin about 45°	Oblique; angle of chin about 45°	Oblique; angle of chin about 45°	Subvertical
Slope of lachrymal edge	Downward and backward	Downward and backward	Downward and backward	Downward and forward
Body axis	Straight	Straight	Straight	Angulated (as in <i>Gambusia</i>)
Water level usually occupied	Below surface	In bottom	Below surface	Surface
Dorsal-fin origin <i>re</i> anal-fin origin	Far ahead	Usually less far ahead	Far ahead	Well behind

TABLE 1
(Continued)

Character	<i>Lucania (Lucania) parva</i>	<i>Lucania (Lucania) interioris</i>	<i>Lucania (Chriopeops) goodii</i>	<i>Leptolucania ommata</i>
Dorsal rays	9-14	10-12	9-12	6 or 7
Scale rows on cheek	2 or 3	2 or 3	2 or 3	1
Interspace between eye and upper preopercular margin	Moderate	Moderate	Moderate	Very narrow
Preopercular pores ²	Usually 7 (variable in north)	0-10	6-8 (predominantly 7)	3-5
Supraorbital canal ²	Complete (typically with 7 pores) to variously incomplete	Variably incomplete to absent	Complete, with 7 pores	Incomplete (only 2 pores, nos. 6 and 7)
Lachrymal pores ²	0-5 (often to usually present)	Absent (very rarely 2)	3-4, usually 4	Absent
Mandibular pores ²	0-5 (occasionally to frequently present)	Absent (very rarely 2)	Absent	Absent
Color pattern	Plain; cross-hatched; often with dusky blotches ³	Plain; cross-hatched; without dusky blotches	Conspicuous longitudinal striping ³	Males with vertical bars; females with lateral spot and precaudal ocellus

¹ Hubbs, 1924 (section III, on *Profundulus*) and 1926.² Gosline, 1949.³ For further details, see Hubbs, Walker, and Johnson, 1943:9-14, pls. 4-6.

TABLE 2

VARIATION IN NUMBER OF DORSAL RAYS IN *Lucania parva* AND *L. interioris*
 Total ray count, including last two elements as one ray. Data graphed in Figures 2 and 3

	9	10	11	12	13	14	No.	Mean	SD	2 SE
<i>Lucania parva</i>										
Atlantic Coast										
Southern New England	-	4	54	15	-	1	74	11.19	0.76	0.18
Long Island (Mill Creek)	-	3	19	5	-	-	27	11.07	0.54	0.20
Chesapeake Bay	-	13	37	2	-	-	52	10.79	0.49	0.14
North Carolina	-	2	16	2	-	-	20	11.00	0.45	0.20
Florida										
Florida Keys	-	2	17	6	-	-	25	11.16	0.54	0.22
Bird (Indian) Key	-	2	9	8	1	-	20	11.40	0.84	0.37
Bays and keys, W. coast	-	11	12	4	-	-	27	10.74	0.70	0.27
Pensacola Bay	1	11	37	6	-	-	55	10.87	0.60	0.16
Coast, Wakulla Co. ¹	-	1	23	11	1	-	36	11.33	0.58	0.19
Mill Creek, Bradenton	-	4	18	6	-	-	28	11.07	0.59	0.22
Slough of St. Johns R.	-	-	13	13	1	-	27	11.56	0.57	0.22
Salt Springs Creek	-	1	19	10	2	-	32	11.41	0.65	0.23
Juniper Springs Cr.	-	1	7	14	5	-	27	11.85	0.68	0.26
TOTAL FOR FLORIDA ²	2	33	159	79	10	-	283	11.22	0.72	0.09
Gulf of México										
Alabama (Big Lake)	-	9	8	6	1	-	24	10.96	0.89	0.36
Mississippi	-	17	69	33	1	-	120	11.15	0.65	0.12
Lake Pontchartrain, La.	-	11	47	18	1	-	77	11.12	0.64	0.15
Mississippi Delta	-	16	68	45	3	1	133	11.29	0.73	0.13
Texas Coast	-	5	43	21	-	-	69	11.23	0.57	0.14
Río Grande, near mouth	-	12	19	4	1	-	36	10.83	0.73	0.24
Río Pánuco, near mouth	-	-	2	1	-	-	3	11.33	-	-
Pecos R., Texas and N. M.	1	67	182	13	1	-	264	10.80	0.54	0.07
Western United States										
Timpie Springs, Utah	2	30	51	7	-	-	90	10.70	0.64	0.13
Blue Lake, Utah	-	4	6	-	-	-	10	10.60	0.49	0.31
Irvine Lake, California	-	1	2	-	-	-	3	10.67	-	-
Yaquina Bay, Oregon	-	18	15	-	-	-	33	10.45	0.51	0.18
San Francisco Bay	2	117	234	23	-	-	376	10.74	0.57	0.06
<i>Lucania interioris</i>										
Ferriño's Canal	-	6	2	-	-	-	8	10.25	0.43	0.31
Los Positos	-	1	4	-	-	-	5	10.80	0.40	0.36
Marsh's material	-	2	7	1	-	-	10	10.90	0.54	0.38
La Angostura Canal	-	10	-	1	-	-	11	10.18	0.58	0.34
Río Garabatal	-	43	58	-	-	-	101	10.57	0.49	0.10
GRAND TOTALS										
<i>Lucania parva</i>	7	362	1,031	274	18	2	1,694	10.96	0.67	0.03
<i>Lucania interioris</i>	-	62	71	2	-	-	135	10.56	0.53	0.09

¹ Counts in part from those summarized by Hubbs, Walker, and Johnson (1943, table 4).

² Including five specimens from Myakka River and one from near Atlantic Beach.

TABLE 3

VARIATION IN NUMBER OF UNBRANCHED AND OF BRANCHED DORSAL RAYS IN *Lucania parva*
AND *L. interioris*

	Unbranched Rays						Branched Rays						
	1	2	3	4	No.	Mean	7	8	9	10	11	No.	Mean
<i>Lucania parva</i>	11	253	43	2	309	2.12	6	75	174	47	7	309	8.92
<i>Lucania interioris</i>	7	34	3	-	44	1.91	1	16	25	1	1	44	8.66
Ferriño's Canal	6	1	-	-	7	1.14	-	1	4	1	1	7	9.29
Los Positos	1	4	-	-	5	1.80	-	-	5	-	-	5	9.00
Marsh's material	-	3	1	-	4	2.25	-	-	4	-	-	4	9.00
La Angostura Canal ..	-	8	1	-	9	2.11	-	8	1	-	-	9	8.11
Río Garabatal	-	18	1	-	19	2.05	1	7	11	-	-	19	8.53

TABLE 4

VARIATION IN NUMBER OF ANAL RAYS IN *Lucania parva* AND *L. interioris*
 Total ray count, including last two elements as one ray. Data graphed in Figures 2 and 3

	8	9	10	11	12	13	No.	Mean	SD	2 SE
<i>Lucania parva</i>										
Atlantic Coast										
Southern New England	1	37	35	3	-	-	76	9.53	0.60	0.14
Long Island (Mill Creek)	1	8	18	-	-	-	27	9.63	0.55	0.21
Chesapeake Bay	2	36	15	-	-	-	53	9.25	0.51	0.14
North Carolina	-	13	6	1	-	-	20	9.40	0.58	0.27
Florida										
Florida Keys	-	14	10	1	-	-	25	9.48	0.57	0.23
Bird (Indian) Key	-	4	9	7	-	-	20	10.15	0.73	0.32
Bays and keys, W. coast	1	17	9	-	-	-	27	9.30	0.53	0.20
Pensacola Bay	-	29	25	1	-	-	55	9.49	0.54	0.14
Coast, Wakulla Co.	-	7	26	3	-	-	36	9.89	0.52	0.17
Mill Creek, Bradenton	1 ¹	8	19	-	-	-	28	9.64	0.55	0.21
Slough of St. Johns R.	1	6	14	6	-	-	27	9.93	0.77	0.30
Salt Springs Creek	-	8	20	4	-	-	32	9.87	0.60	0.21
Juniper Springs Cr.	-	3	21	3	-	-	27	10.00	0.47	0.18
TOTAL FOR FLORIDA ²	3	98	157	25	-	-	283	9.72	0.63	0.08
Gulf of México										
Alabama (Big Lacc)	-	9	13	2	-	-	24	9.71	0.61	0.25
Mississippi	-	34	71	15	-	-	120	9.84	0.62	0.11
Lacc Pontchartrain, La.	-	19	47	11	-	-	77	9.90	0.62	0.14
Mississippi Delta, La.	-	33	79	21	-	-	133	9.91	0.63	0.09
Texas Coast	-	8	51	9	1	-	69	10.06	0.59	0.14
Río Grande, near mouth	-	19	15	2	-	-	36	9.53	0.60	0.20
Río Pánuco, near mouth	-	-	3	-	-	-	3	10.00	-	-
Pecos R., Texas and N.M.	7	187	67	1	1	1	264	9.26	0.57	0.07
Western United States										
Timpic Springs, Utah	3	57	30	1	-	-	91	9.32	0.55	0.12
Blue Lake, Utah	-	8	2	-	-	-	10	9.20	0.40	0.25
Irvine Lake, California	1	2	-	-	-	-	3	8.67	-	-
Yaquina Bay, Oregon	11	22	1	-	-	-	34	8.71	0.52	0.17
San Francisco Bay	19	278	79	-	-	-	376	9.16	0.48	0.05
<i>Lucania interioris</i>										
Ferrifo's Canal	-	6	2	-	-	-	8	9.25	0.43	0.31
Los Positos	-	3	2	-	-	-	5	9.40	0.49	0.44
Marsh's material	-	5	5	-	-	-	10	9.50	0.50	0.32
La Angostura Canal	-	7	4	-	-	-	11	9.36	0.48	0.29
Río Garabatal	-	50	50	1	-	-	101	9.51	0.52	0.10
GRAND TOTALS										
<i>Lucania parva</i>	48	868	689	91	1	2	1,699	9.49	0.66	0.03
<i>Lucania interioris</i>	-	71	63	1	-	-	135	9.48	0.51	0.09

¹ This count of 8 rays is for an anal fin beside the end of which, on one side, is an accessory fin with 5 rays on an oblique base; the two fins end close together.

² The total for Florida includes five specimens from Myakka River and one from near Atlantic Beach.

TABLE 5
 VARIATION IN NUMBER OF UNBRANCHED AND OF BRANCHED ANAL RAYS IN *Lucania parva*
 AND *L. interioris*

	Unbranched Rays				Branched Rays				Mean	SD	2 SE					
	1	2	3	4	5	6	7	8				9	10	No.		
<i>Lucania parva</i>																
Atlantic Coast																
Southern New England	6	2	1	—	9	1.44	—	2	5	2	—	9	8.00	0.66	0.44	
Long Island (Mill Creek)	9	10	—	—	19	1.53	—	2	7	9	—	18	8.39	0.68	0.32	
Chesapeake Bay	16	4	—	—	20	1.20	—	1	2	7	10	—	20	8.30	0.84	0.38
Florida																
Florida Keys	17	8	—	—	25	1.32	—	4	14	6	1	25	8.16	0.83	0.33	
Bird (Indian) Key	10	10	—	—	20	1.50	—	1	9	6	4	20	8.65	0.85	0.38	
Pensacola Bay	11	10	—	—	21	1.48	—	4	11	5	1	21	8.14	0.77	0.34	
Coast, Wakulla Co.	9	13	—	—	22	1.59	—	1	13	8	—	22	8.32	0.55	0.23	
Juniper Springs Cr.	4	4	—	—	8	1.50	—	—	5	3	—	8	8.38	0.48	0.34	
TOTAL FOR FLORIDA	51	45	—	—	96	1.47	—	10	52	28	6	96	8.31	0.74	0.15	
Gulf of México																
Lake Pontchartrain, La.	14	6	—	—	20	1.30	—	—	9	9	2	20	8.65	0.65	0.29	
Texas Coast	4	22	—	—	26	1.85	—	2	17	5	2	26	8.27	0.78	0.31	
Río Grande, near mouth	6	19	1	—	26	1.81	—	—	9	14	3	—	26	7.77	0.64	0.25
Pecos R., Texas and																
N. M.	24	23	1	1	49	1.57	1	—	15	30	3	—	49	7.69	0.68	0.19
Western United States																
Timpic Springs, Utah	23	11	—	—	34	1.32	—	—	5	21	8	—	34	8.09	0.61	0.21
Yaquina Bay, Oregon	6	2	—	—	8	1.25	—	—	4	4	—	—	8	7.50	0.53	0.38
<i>Lucania interioris</i>																
Ferrño's Canal	7	1	—	—	8	1.13	—	—	1	5	2	—	8	8.13	0.60	0.42
Los Positos	1	4	—	—	5	1.80	—	—	3	1	1	—	5	7.60	0.80	0.72
Marsh's material	—	2	1	—	3	2.33	—	—	2	1	—	—	3	7.33	—	—
La Angostura Canal	—	8	1	—	9	2.11	—	—	8	1	—	—	9	7.11	0.31	0.21
Río Garabatal	5	13	—	—	18	1.72	—	—	7	8	3	—	18	7.78	0.71	0.34
GRAND TOTALS																
<i>Lucania parva</i> ¹	160	144	3	1	308	1.50	1	1	51	167	77	10	307	8.13	0.76	0.09
<i>Lucania interioris</i>	13	28	2	—	43	1.74	—	—	21	16	6	—	43	8.65	0.71	0.22

¹ Including one specimen from Irvine Lake, California, with 1 unbranched and 8 branched rays.

TABLE 6

CORRELATION BETWEEN NUMBER OF DORSAL AND ANAL RAYS IN *Lucania parva* AND *L. interioris*
(See also Figure 3)

	Dorsal Rays	Number of Rays in Anal Fin						
		8	9	10	11	12	13	
<i>Lucania parva</i>								
Lake Pontchartrain,	10	-	9	2	-	-	-	N = 77
Louisiana	11	-	10	32	5	-	-	
(one collection)	12	-	-	13	5	-	-	$r = 0.55 \pm 0.08$
	13	-	-	-	1	-	-	
Mississippi Delta,	10	-	14	2	-	-	-	N = 132
Louisiana	11	-	17	47	4	-	-	
(one collection)	12	-	2	29	14	-	-	$r = 0.58 \pm 0.06$
	13	-	-	1	2	-	-	
Pecos River, Texas	9	1	-	-	-	-	-	N = 263
and New Mexico	10	4	59	3	-	-	1	
(several collections)	11	2	122	56	1	1	-	$r = 0.26 \pm 0.06$
	12	-	6	7	-	-	-	
Timpie Springs,	9	-	1	-	-	-	-	N = 90
Tooele County, Utah	10	3	24	4	-	-	-	
(two collections)	11	-	26	24	1	-	-	$r = 0.34 \pm 0.09$
	12	-	4	3	-	-	-	
About San Francisco Bay,	9	1	1	-	-	-	-	N = 376
California	10	17	97	3	-	-	-	
(several collections)	11	1	175	58	-	-	-	$r = 0.47 \pm 0.03$
	12	-	5	18	-	-	-	
<i>Lucania interioris</i>								
Río Garabatal	10	-	30	13	-	-	-	N = 101
	11	-	20	37	1	-	-	$r = 0.35 \pm 0.09$

TABLE 7

VARIATION IN NUMBER OF PRINCIPAL CAUDAL RAYS IN *Lucania parva* AND *L. interioris*
 Included are one unbranched ray on upper and one on lower margin. Data graphed in
 Figure 4

	12	13	14	15	16	17	18	No.	Mean	SD	2 SE
<i>Lucania parva</i>											
Atlantic Coast											
Southern New England	-	-	-	-	7	2	-	9	16.22	0.42	0.28
Long Island (Mill Creek)	-	-	1	3	11	3	-	18	15.89	0.74	0.35
Chesapeake Bay	-	-	-	6	12	2	-	20	15.80	0.60	0.27
Florida											
Florida Keys	-	-	7	6	8	-	-	21	15.05	0.83	0.36
Bird (Indian) Key	-	-	5	5	8	2	-	20	15.35	0.96	0.43
Pensacola Bay	2	-	11	5	3	-	-	21	14.33	1.04	0.45
Coast, Wakulla Co.	-	-	3	5	32	1	2	43	15.86	0.77	0.23
Juniper Springs Cr.	-	-	-	3	1	1	-	5	15.60	0.80	0.72
TOTAL FOR FLORIDA	2	-	26	24	52	4	2	110	15.31	1.04	0.20
Gulf of México											
Lake Pontchartrain, La.	-	-	7	5	8	-	-	20	15.05	0.86	0.39
Texas Coast	-	-	2	4	18	3	-	27	15.81	0.72	0.28
Río Grande, near mouth	-	-	4	9	18	2	-	33	15.55	0.78	0.27
Río Pánuco, near mouth	-	-	1	1	1	-	-	3	15.00	-	-
Pecos R., Texas and N. M.	-	-	-	11	26	7	3	47	16.04	0.80	0.23
Western United States											
Timpic Springs, Utah	-	-	2	10	13	7	2	34	15.91	0.98	0.33
Irvine Lake, California	-	-	-	-	-	-	1	1	18.0?	-	-
Yaquina Bay, Oregon	-	-	-	-	16	1	1	18	16.17	0.51	0.24
San Francisco Bay	-	-	1	5	20	5	-	31	15.94	0.67	0.24
<i>Lucania interioris</i>											
Ferriño's Canal	-	-	1	-	2	2	2	7	16.57	1.29	0.98
Los Positos	-	-	1	2	-	1	1	5	15.80	1.47	1.31
Marsh's material	-	-	1	1	2	-	-	4	15.25	-	-
La Angostura Canal	-	-	1	5	2	-	-	8	15.12	0.61	0.43
Río Garabatal	-	-	6	3	8	2	-	19	15.32	1.03	0.47
GRAND TOTALS											
<i>Lucania parva</i>	2	-	44	78	202	36	9	371	15.68	0.93	0.10
<i>Lucania interioris</i>	-	-	10	11	14	5	3	43	15.53	1.23	0.37

TABLE 8
 VARIATION IN NUMBER OF PECTORAL RAYS IN *Lucania parva* AND *L. interioris*
 Data graphed in Figure 4

	10	11	12	13	14	15	No.	Mean	SD	2 SE
<i>Lucania parva</i>										
Atlantic Coast										
Southern New England	-	-	-	4	14	-	18	13.78	0.42	0.23
Long Island (Mill Creek)	-	-	-	25	15	-	40	13.37	0.48	0.18
Chesapeake Bay	-	-	-	33	7	-	40	13.17	0.38	0.14
Florida										
Florida Keys	-	-	8	33	9	-	50	13.02	0.58	0.19
Bird (Indian) Key	-	-	5	22	13	-	40	13.20	0.64	0.23
Pensacola Bay	-	-	8	18	16	-	42	13.19	0.73	0.26
Coast, Wakulla Co. ¹	-	1	3	37	28	3	72	13.40	0.70	0.19
Juniper Springs Cr.	-	-	-	5	17	-	22	13.77	0.42	0.21
TOTAL FOR FLORIDA	-	1	24	115	83	3	226	13.28	0.68	0.11
Gulf of México										
Lake Pontchartrain, La.	-	-	12	24	4	-	40	12.80	0.60	0.22
Texas Coast	-	-	-	18	33	3	54	13.72	0.56	0.18
Río Grande, near mouth	-	-	1	24	34	1	60	13.58	0.56	0.17
Río Pánuco, near mouth	-	-	-	3	1	-	4	13.25	-	-
Pecos R., Texas and N. M.	-	-	1	85	44	-	130	13.33	0.49	0.09
Western United States										
Timpic Springs, Utah	1	-	5	42	19	-	67	13.16	0.68	0.19
Blue Lake, Utah	-	-	-	8	-	-	8	13.00	-	-
Irvine Lake, California	-	-	-	2	-	-	2	13.0?	-	-
Yaquina Bay, Oregon	-	-	5	25	4	-	34	12.97	0.52	0.20
San Francisco Bay	-	-	1	36	28	1	66	13.44	0.55	0.16
<i>Lucania interioris</i>										
Ferriño's Canal	-	-	-	2	4	10	16	14.50	0.71	0.41
Los Positos	-	-	-	2	8	-	10	13.80	0.40	0.29
Marsh's material	-	-	-	-	10	5	15	14.33	0.47	0.28
La Angostura Canal	-	-	-	-	10	8	18	14.44	0.50	0.27
Río Garabatal	-	-	-	5	32	3	40	13.95	0.44	0.16
GRAND TOTALS										
<i>Lucania parva</i>	1	1	49	444	286	8	789	13.31	0.62	0.04
<i>Lucania interioris</i>	-	-	-	9	64	26	99	14.17	0.57	0.13

¹ Counts in part from those summarized by Hubbs, Walker, and Johnson, 1943, table 4.

TABLE 9

ANALYSIS OF ASYMMETRY IN THE NUMBER OF PECTORAL RAYS IN *Lucania parva*
AND *L. interioris*

	<i>L. parva</i>	<i>L. interioris</i>
Number of fish with counts:		
Equal on the two sides	289 (78%)	36 (73%)
Higher on the left side	35 (9%)	5 (10%)
Higher on the right side	47 (13%)	8 (16%)
Length of lowest ray on the side with the higher count compared with length of lowest ray on opposite side:		
Shorter	61 (94%)	12 (100%)
Equal	3 (5%)	- (0%)
Longer	1 (2%)	- (0%)

TABLE 10

VARIATION AND ASYMMETRY IN NUMBER OF PELVIC RAYS IN *Lucania parva* AND *L. interioris*

Species	Number of Rays per Fin					Fish with Counts	
	0	4	5	6	7	Symmetrical No.	Asymmetrical No. (%)
<i>Lucania parva</i>	-	1 (1) ¹	12 (10) ²	702 (17)	11 (7)	344	17 (5%)
<i>Lucania interioris</i>	2 (2)	-	2 (0)	100 (2)	-	50	2 (4%)

¹ The numbers in parentheses represent counts in one fin that differ from the count of rays in the fin on the opposite side of the body. The fins were counted on both sides.

² The 12 fins with 5 rays comprise 8 that are matched by a 6-rayed fin on the opposite side plus 2 fins that are formed, in contact, on the left side of a fish that has 6 rays in the one fin on the right side.

TABLE 11

VARIATION IN NUMBER OF LATERAL SCALE ROWS IN *Lucania parva* AND *L. interioris*
 Counted from gill-slit to structural base of caudal fin (see text)

	23	24	25	26	27	28	29	No.	Mean	SD	2 SE
<i>Lucania parva</i>											
Atlantic Coast											
Southern New England	-	-	-	-	16	3	-	19	27.16	0.36	0.17
Long Island (Mill Creek)	-	-	-	-	10	10	-	20	27.50	0.50	0.22
Chesapeake Bay	-	-	-	-	1	16	3	20	27.10	0.44	0.19
Florida											
Florida Keys	1	1	18	5	-	-	-	25	25.08	0.63	0.25
Bird (Indian) Key	-	1	6	12	1	-	-	20	25.65	0.65	0.29
Pensacola Bay	-	-	-	7	7	5	2	21	27.10	0.97	0.42
Coast, Wakulla Co. ¹	-	-	3	8	10	1	-	22	26.41	0.78	0.33
Juniper Springs Cr.	-	-	-	-	-	3	7	11	27.82	0.57	0.35
TOTAL FOR FLORIDA	1	2	27	32	21	13	3	99	26.22	1.19	0.24
Gulf of México											
Lake Pontchartrain, La.	-	-	-	-	2	16	2	20	27.00	0.45	0.20
Texas Coast	-	-	2	3	11	4	-	20	26.85	0.85	0.38
Río Grande, near mouth	-	-	-	3	24	3	-	30	27.00	0.45	0.16
Río Pánuco, near mouth	-	-	-	-	1	2	-	3	26.67	-	-
Pecos R., Texas and N. M.	-	-	-	-	17	33	2	52	26.71	0.53	0.15
Western United States											
Timpie Springs, Utah	-	-	-	-	-	9	3	12	27.25	0.43	0.25
Blue Lake, Utah	-	-	-	-	-	3	1	4	27.25	-	-
Yaquina Bay, Oregon	-	-	-	-	-	18	5	23	27.21	0.42	0.19
San Francisco Bay	-	-	-	-	-	17	11	28	27.39	0.49	0.18
<i>Lucania interioris</i>											
Ferrifño's Canal	-	-	1	4	3	-	-	8	26.25	0.66	0.47
Los Positos	-	-	-	3	3	-	-	6	26.50	0.50	0.42
Marsh's material	-	-	2	7	1	-	-	10	25.90	0.54	0.34
La Angostura Canal	-	-	1	8	-	-	-	9	25.89	0.31	0.21
Río Garabatal	-	-	6	15	-	-	-	21	25.71	0.45	0.20
GRAND TOTALS											
<i>Lucania parva</i> ²	1	2	29	59	196	61	3	351	26.83	0.88	0.10
<i>Lucania interioris</i>	-	-	10	37	7	-	-	54	25.94	0.54	0.15

¹ Mean (26.41) is close to that (26.24) reported for same region, with some duplication of specimens, by Hubbs, Walker, and Johnson (1943, table 4).

² Including one specimen from Irvine Lake, California, with 28 scale rows.

TABLE 12

VARIATION IN NUMBER OF SCALES BETWEEN ORIGINS OF DORSAL AND ANAL FINS
IN *Lucania parva* AND *L. interioris*

	8	9	10	11	No.	Mean	SD	2 SE
<i>Lucania parva</i>								
Atlantic Coast								
Southern New England	—	6	14	—	20	9.70	0.46	0.20
Long Island (Mill Creek)	—	7	13	—	20	9.65	0.48	0.21
Chesapeake Bay	1	12	7	—	20	9.30	0.56	0.25
Florida								
Florida Keys	—	8	17	—	25	9.68	0.47	0.19
Bird (Indian) Key	1	4	15	—	20	9.70	0.56	0.25
Pensacola Bay	2	16	3	—	21	9.05	0.49	0.21
Coast, Wakulla Co.	—	5	16	1	22	9.82	0.49	0.21
Juniper Springs Cr.	—	4	7	—	11	9.64	0.48	0.29
TOTAL FOR FLORIDA	3	37	58	1	99	9.58	0.57	0.11
Gulf of México								
Lake Pontchartrain, La.	3	16	1	—	20	8.90	0.44	0.19
Texas Coast	3	13	4	—	20	9.05	0.59	0.26
Río Grande, near mouth	3	13	14	—	30	9.37	0.66	0.24
Río Pánuco, near mouth	—	3	—	—	3	9.00	—	—
Pecos R., Texas and N. M.	25	22	5	—	52	8.62	0.89	0.25
Western United States								
Timpie Springs, Utah	5	3	4	—	12	8.92	0.86	0.50
Blue Lake, Utah	—	3	1	—	4	9.25	—	—
Yaquina Bay, Oregon	—	11	12	—	23	9.52	0.51	0.21
San Francisco Bay	—	14	14	—	28	9.50	0.71	0.27
<i>Lucania interioris</i>								
Ferriño's Canal	—	3	5	—	8	9.62	0.48	0.34
Los Positos	—	5	—	—	5	9.00	—	—
Marsh's material	1	6	3	—	10	9.20	0.60	0.38
La Angostura Canal	—	4	5	—	9	9.56	0.50	0.33
Río Garabatal	—	11	9	—	20	9.45	0.50	0.22
GRAND TOTALS								
<i>Lucania parva</i> ¹	43	161	147	1	352	9.30	0.68	0.07
<i>Lucania interioris</i>	1	29	22	—	52	9.40	0.75	0.21

¹ Including one specimen from Irvine Lake, California, with 9 scales.

TABLE 13

VARIATION IN NUMBER OF SCALES AROUND BODY IN *Lucania parva* AND *L. interioris*
Data graphed in Figure 5

	18	19	20	21	22	23	24	25	No.	Mean	SD	2 SE
<i>Lucania parva</i>												
Atlantic Coast												
Southern New England	-	-	-	-	2	6	1	-	9	22.89	0.57	0.38
Long Island (Mill Creek)	-	-	-	-	3	15	2	-	20	22.95	0.50	0.22
Chesapeake Bay	-	-	-	-	1	17	2	-	20	23.05	0.38	0.17
Florida												
Florida Keys	-	-	3	-	12	8	2	-	25	22.24	1.14	0.46
Bird (Indian) Key	-	-	1	3	1	14	-	1	20	22.60	1.07	0.48
Pensacola Bay	1	-	9	8	3	-	-	-	21	20.57	0.90	0.39
Coast, Wakulla Co. ¹	-	-	3	4	24	5	-	-	36	21.86	0.75	0.25
Juniper Springs Cr.	-	-	-	6	2	3	-	-	11	21.73	0.86	0.52
TOTAL FOR FLORIDA	1	-	16	21	42	30	2	1	113	21.82	1.13	0.21
Gulf of México												
Lake Pontchartrain, La.	-	-	9	8	1	2	-	-	20	20.80	0.93	0.41
Texas Coast	-	-	6	4	3	3	-	-	16	21.19	1.13	0.57
Río Grande, near mouth	-	1	8	12	4	5	-	-	30	21.13	1.09	0.40
Río Pánuco, near mouth	-	1	-	-	1	-	-	-	2	20.50	-	-
Pecos R., Texas and N. M. ..	-	-	9	16	5	3	-	-	33	21.06	0.89	0.31
Western United States												
Timpie Springs, Utah	-	-	-	5	1	6	-	-	12	22.08	0.95	0.55
Blue Lake, Utah	-	-	3	-	1	-	-	-	4	20.50	-	-
Yaquina Bay, Oregon	-	-	-	-	4	17	-	-	21	22.81	0.40	0.19
San Francisco Bay	-	-	-	1	11	22	4	-	28	23.04	0.57	0.21
<i>Lucania interioris</i>												
Ferriño's Canal	-	-	-	1	1	4	1	-	7	22.71	0.88	0.66
Los Positos	-	-	-	2	3	-	-	-	5	21.60	0.49	0.44
Marsh's material	-	-	-	-	10	-	-	-	10	22.00	-	-
La Angostura Canal	-	-	-	1	4	4	-	-	9	22.33	0.67	0.44
Río Garabatal	-	-	-	-	8	8	4	-	20	22.80	0.75	0.33
GRAND TOTALS												
<i>Lucania parva</i> ²	1	2	51	67	69	127	11	1	329	21.92	1.21	0.13
<i>Lucania interioris</i>	-	-	-	4	26	16	5	-	51	22.43	0.77	0.22

¹ Counts in part from those summarized by Hubbs, Walker, and Johnson (1943, table 4).

² Including one specimen from Irvine Lake, California, with 23 scales.

TABLE 14

VARIATION IN NUMBER OF SCALES AROUND CAUDAL PEDUNCLE IN *Lucania parva*
AND *L. interioris*

	11	12	13	14	15	16	No.	Mean
<i>Lucania parva</i>								
Atlantic Coast								
Southern New England	-	-	-	-	2	7	9	15.78
Long Island (Mill Creek)	-	-	-	-	-	20	20	16.00
Chesapeake Bay	-	-	-	1	2	17	20	15.80
Florida								
Florida Keys	-	2	-	3	5	15	25	15.24
Bird (Indian) Key	-	-	-	-	-	20	20	16.00
Pensacola Bay	1	10	1	2	1	6	21	13.48
Coast, Wakulla Co.	-	2	-	2	2	16	22	15.36
Juniper Springs Cr.	-	-	-	1	-	10	11	15.82
TOTAL FOR FLORIDA	1	14	1	8	8	67	99	15.11
Gulf of México								
Lake Pontchartrain, La.	-	7	-	4	3	6	20	14.05
Texas Coast	-	7	3	2	1	3	16	13.37
Río Grande, near mouth	-	14	4	4	3	5	30	13.37
Río Pánuco, near mouth	-	3	-	-	-	-	3	12.00
Pecos R., Texas and N. M.	-	1	4	12	12	4	33	14.42
Western United States								
Timpie Springs, Utah	-	-	-	1	3	8	12	15.58
Blue Lake, Utah	-	-	-	1	1	2	4	15.25
Yaquina Bay, Oregon	-	-	-	-	-	22	22	16.00
San Francisco Bay	-	-	-	-	1	27	28	15.96
<i>Lucania interioris</i>								
Ferriño's Canal	-	-	-	2	1	5	8	15.37
Los Positos	-	-	-	1	2	2	5	15.20
Marsh's material	-	-	-	-	-	10	10	16.00
La Angostura Canal	-	-	-	-	-	9	9	16.00
Río Garabatal	-	-	-	-	2	18	20	15.90
GRAND TOTALS								
<i>Lucania parva</i> ¹	1	46	12	33	36	189	317	14.97
<i>Lucania interioris</i>	-	-	-	3	5	44	52	15.79

¹ Including one specimen from Irvine Lake, California with 16 scales.

TABLE 15

VARIATION IN NUMBER OF VERTEBRAE IN *Lucania parva* AND *L. interioris*
Data graphed in Figure 6

	25	26	27	28	29	30	No.	Mean
<i>Lucania parva</i>								
Atlantic Coast								
Southern New England	-	-	-	7	-	-	7	28.00
Long Island (Mill Creek)	-	-	2	17	1	-	20	27.95
Chesapeake Bay	-	-	4	15	-	-	19	27.79
Florida								
Florida Keys	4	16	3	-	-	-	23	25.96
Bird (Indian) Key	1	8	10	1	-	-	20	26.55
Pensacola Bay	-	1	11	5	3	1	21	27.62
Juniper Springs Cr.	-	-	-	7	13	-	20	28.65
TOTAL FOR FLORIDA	5	25	24	13	16	1	84	27.15
Gulf of México								
Lake Pontchartrain, La.	-	-	7	12	1	-	20	27.70
Texas Coast	-	-	7	12	15	-	34	28.24
Río Grande, near mouth	-	-	1	2	-	-	3	27.67
Pecos R., Texas and N. M.	-	-	2	23	1	-	26	27.96
Western United States								
Timpie Springs, Utah	-	-	1	9	3	-	13	28.15
Blue Lake, Utah	-	-	1	6	2	-	9	28.11
Yaquina Bay, Oregon	-	-	3	26	1	-	30	27.93
San Francisco Bay	-	-	4	23	1	-	28	27.89
<i>Lucania interioris</i>								
Ferriño's Canal	-	-	3	3	-	-	6	27.50
Los Positos	-	-	3	2	-	-	5	27.40
Marsh's material	-	1	3	-	-	-	4	26.75
La Angostura Canal	-	1	3	-	-	-	4	26.75
Río Garabatal	-	8	12	-	-	-	20	26.60
GRAND TOTALS								
<i>Lucania parva</i> ¹	5	25	56	166	41	1	294	27.73
<i>Lucania interioris</i>	-	10	24	5	-	-	39	26.87

¹ Including one specimen from Irvine Lake, California, with 28 vertebrae.

TABLE 16

VARIATION IN NUMBER OF PREOPERULAR PORES IN *Lucania parva* AND *L. interioris*
Data graphed in Figure 7. Both sides were counted

	0	1	2	3	4	5	6	7	8	9	10	No.	Mean	Percentage			
														0-4	5-6	7	8-10
<i>Lucania parva</i>																	
Atlantic Coast																	
Southern New																	
England	5	-	-	1	6	5	1	31	23	7	3	82	6.85	15	7	38	40
Long Island (Mill Creek)	-	-	1	-	2	-	4	11	16	6	-	40	7.33	7.5	10	27.5	55
Chesapeake Bay	-	-	-	-	-	-	1	34	5	-	-	40	7.10	0	2.5	85	12.5
Florida																	
Florida Keys	-	-	-	-	-	-	-	50	-	-	-	50	7.00	0	0	100	0
Bird (Indian) Key	-	-	-	-	-	-	-	40	-	-	-	40	7.00	0	0	100	0
Pensacola Bay	-	-	-	-	-	-	1	39	2	-	-	42	7.02	0	2	93	5
Coast, Wakulla Co.	-	-	-	-	-	-	-	40	4	-	-	44	7.09	0	0	91	9
Juniper Springs Cr.	-	-	-	-	-	-	-	19	3	-	-	22	7.14	0	0	86	14
TOTAL FOR FLORIDA	-	-	-	-	-	-	1	188	9	-	-	198	7.04	0	1	95	5
Gulf of México																	
Lake Pontchartrain,																	
La.	-	-	-	-	-	-	1	39	-	-	-	40	6.97	0	2.5	97.5	0
Texas Coast	-	-	-	-	-	-	-	54	-	-	-	54	7.00	0	0	100	0
Río Grande, near mouth	-	-	-	-	-	-	1	59	-	-	-	60	6.98	0	2	98	0
Río Pánuco, near mouth	-	-	-	-	-	-	-	6	-	-	-	6	7.00	0	0	100	0
Pecos R., Texas and N. M.	-	-	-	-	-	-	2	63	31	2	-	98	7.34	0	2	64	34
Western United States																	
Timpie Springs,																	
Utah	-	-	-	-	1	1	49	16	1	-	-	68	7.22	0	3	72	25
Blue Lake, Utah	-	-	-	-	-	-	8	2	-	-	-	10	7.20	0	0	80	20
Yaquina Bay, Oregon	5	-	8	3	2	3	2	10	6	3	-	42	4.88	43	12	24	21
San Francisco Bay ..	-	-	-	-	1	-	2	32	15	5	1	56	7.41	2	4	57	37
<i>Lucania interioris</i>																	
Ferriño's Canal	-	-	-	-	1	1	3	4	6	1	-	16	8.00	0	12.5	19	69
Los Positos	-	-	-	-	-	-	2	1	3	4	-	10	8.90	0	0	20	80
Marsh's material	-	-	-	-	-	-	2	5	7	2	-	16	8.56	0	0	12.5	87.5
La Angostura Canal	3	-	3	5	1	2	2	1	-	-	-	17	3.18	71	24	6	0
Río Garabatal	8	-	3	10	1	3	2	2	9	2	-	40	4.27	55	12.5	5	27.5
GRAND TOTALS																	
<i>Lucania parva</i> ¹	10	-	9	4	11	9	16	586	123	24	4	796	6.98	4	3	74	19
<i>Lucania interioris</i>	11	-	6	15	2	6	5	10	19	18	7	99	5.85	34	11	10	44

¹ Including one specimen from Irvine Lake, California, with 7 pores on each side.

TABLE 17

VARIATION IN NUMBER OF SUPRAORBITAL PORES IN *Lucania parva* AND *L. interioris*
Data graphed in Figure 7. Both sides were counted

	0	1	2	3	4	5	6	7	8	9	10	11	No.	Mean	Percentage			
															0-4	5-6	7	8-11
<i>Lucania parva</i>																		
Atlantic Coast																		
Southern New																		
England	8	1	4	1	3	1	11	5	14	19	2	13	82	7.04	21	15	6	59
Long Island (Mill Creek)	-	-	-	-	6	-	8	4	3	11	2	2	36	7.36	17	22	11	50
Chesapeake Bay ...	-	-	-	-	-	1	13	11	12	2	1	40	8.10	0	2.5	32.5	65	
Florida																		
Florida Keys	-	-	-	-	1	-	49	-	-	-	-	50	6.96	0	2	98	0	
Bird (Indian) Key..	-	-	-	-	-	-	40	-	-	-	-	40	7.00	0	0	100	0	
Pensacola Bay	-	-	-	-	-	1	39	2	-	-	-	42	7.02	0	2	93	5	
Coast, Wakulla Co.	-	-	-	-	-	-	44	-	-	-	-	44	7.00	0	0	100	0	
Juniper Springs Cr.	-	-	-	-	-	-	22	-	-	-	-	22	7.00	0	0	100	0	
TOTAL FOR FLORIDA	-	-	-	-	1	1	184	2	-	-	-	188	6.99	0	1	98	1	
Gulf of México																		
Lake Pontchartrain,																		
La.	-	-	-	-	-	-	40	-	-	-	-	40	7.00	0	0	100	0	
Texas Coast	-	-	-	-	-	-	54	-	-	-	-	54	7.00	0	0	100	0	
Río Grande, near mouth	-	-	-	-	-	2	54	4	-	-	-	60	7.03	0	3	90	7	
Río Pánuco, near mouth	-	-	-	-	-	1	2	1	-	-	-	4	7.00	0	25	50	25	
Pecos R., Texas and N. M.	-	-	-	-	-	-	58	25	10	3	2	98	7.63	0	0	59	41	
Western United States																		
Timpie Springs,																		
Utah	-	-	-	-	-	1	55	11	1	-	-	68	7.18	0	1	81	18	
Blue Lake, Utah ¹ ..	-	-	-	-	1	3	6	-	-	-	-	10	6.50	0	40	60	0	
Yaquina Bay, Ore- gon ¹	5	-	5	1	5	1	6	8	5	3	1	2	42	5.45	38	17	19	26
San Francisco Bay..	-	-	-	-	2	1	1	11	14	14	8	5	56	8.37	4	4	20	73
<i>Lucania interioris</i>																		
Ferriño's Canal	2	-	10	-	3	-	1	-	-	-	-	-	16	2.37	94	6	0	0
Los Positos	1	-	3	-	3	-	2	-	1	-	-	-	10	3.80	70	20	0	10
Marsh's material ..	4	-	7	-	2	-	-	-	-	-	-	-	13	1.69	100	0	0	0
La Angostura Canal	14	-	3	-	1	-	-	-	-	-	-	-	18	0.56	100	0	0	0
Río Garabatal	32	-	6	-	2	-	-	-	-	-	-	-	40	0.50	100	0	0	0
GRAND TOTALS																		
<i>Lucania parva</i> ²	13	1	9	2	16	5	35	504	90	71	19	25	790	7.19	5	5	64	26
<i>Lucania interioris</i> ...	53	-	29	-	11	-	3	-	1	-	-	-	97	1.32	96	3	0	1

¹ Small size of these specimens may explain the low counts.

² Including one specimen from Irvine Lake, California, with 9 pores on one side and 10 on the other side.

TABLE 18

VARIATION IN NUMBER OF LACHRYMAL PORES IN *Lucania parva* AND *L. interioris*
Data graphed in Figure 7. Both sides were counted

	0	1	2	3	4	5	No.	Mean	Percentage		
									0	1, 2, 3, or 5	4
<i>Lucania parva</i>											
Atlantic Coast											
Southern New England	47	-	29	-	5	1	82	1.01	57	37	6
Long Island (Mill Creek) ..	18	-	19	-	3	-	40	1.25	45	47.5	7.5
Chesapeake Bay	22	-	12	-	2	4	40	1.30	55	40	5
Florida											
Florida Keys	5	-	1	1	42	1	50	3.56	10	6	84
Bird (Indian) Key	-	-	-	-	40	-	40	4.00	0	0	100
Pensacola Bay	21	-	1	1	16	3	42	2.00	50	12	38
Coast, Wakulla Co.	-	-	-	2	41	1	44	3.98	0	7	93
Juniper Springs Cr.	-	-	-	-	20	2	22	4.09	0	9	91
TOTAL FOR FLORIDA	26	-	2	4	159	7	198	3.47	13	7	80
Gulf of México											
Lake Pontchartrain, La.	7	-	12	3	17	1	40	2.65	17.5	40	42.5
Texas Coast	7	-	2	3	40	2	54	3.39	13	13	74
Río Grande, near mouth ..	2	-	8	6	41	3	60	3.55	3	28	68
Río Pánuco, near mouth ¹ ..	5	-	1	-	-	-	6	0.33	83	17	0
Pecos R., Texas and N. M.	42	-	16	3	17	20	98	2.13	43	40	17
Western United States											
Timpie Springs, Utah ²	-	-	11	6	38	13	68	3.78	0	44	56
Blue Lake, Utah ¹	8	-	1	1	-	-	10	0.50	80	20	0
Yaquina Bay, Oregon ¹	32	3	5	-	2	-	42	0.50	76	19	5
San Francisco Bay	15	-	17	-	18	6	56	2.43	27	41	32
<i>Lucania interioris</i>											
Ferriño's Canal	16	-	-	-	-	-	16	0	100	0	0
Los Positos	8	-	2	-	-	-	10	0.40	80	20	0
Marsh's material	16	-	-	-	-	-	16	0	100	0	0
La Angostura Canal	18	-	-	-	-	-	18	0	100	0	0
Río Garabatal	40	-	-	-	-	-	40	0	100	0	0
GRAND TOTALS											
<i>Lucania parva</i> ³	233	3	135	26	342	57	796	2.52	29	28	43
<i>Lucania interioris</i>	98	-	2	-	-	-	100	0.04	98	2	0

¹ Low count may be due largely or wholly to small size of specimens counted.

² High count may be attributed in part at least to large size and high development of most of the specimens counted.

³ Including one specimen from Irvine Lake, California, with no pores on either side.

TABLE 19
 VARIATION IN NUMBER OF MANDIBULAR PORES IN *Lucania parva* AND *L. interioris*
 Data graphed in Figure 7. Both sides were counted

	0	1	2	3	4	5	6	No.	Mean	Percentage			
										0	1-3	4	5-6
<i>Lucania parva</i>													
Atlantic Coast													
Southern New England	81	-	1	-	-	-	-	82	0.02	99	1	0	0
Long Island (Mill Creek) ..	33	-	5	1	1	-	-	40	0.43	82.5	15	2.5	0
Chesapeake Bay	32	-	2	4	2	-	-	40	0.60	80	15	5	0
Florida													
Florida Keys	23	-	5	4	9	6	3	50	2.12	46	18	18	18
Bird (Indian) Key	-	-	3	16	7	14	-	40	3.80	0	47.5	17.5	35
Pensacola Bay	32	-	2	7	1	-	-	42	0.69	76	21	2	0
Coast, Wakulla Co.	-	-	3	10	3	28	-	44	4.27	0	30	7	64
Juniper Springs Cr.	-	-	-	1	7	14	-	22	4.59	0	5	32	64
TOTAL FOR FLORIDA	55	-	13	38	27	62	3	198	2.91	28	26	14	33
Gulf of México													
Lake Pontchartrain, La.	35	-	1	4	-	-	-	40	0.35	87.5	12.5	0	0
Texas Coast	51	-	1	2	-	-	-	54	0.11	94	6	0	0
Río Grande, near mouth ..	39	2	8	8	-	3	-	60	0.95	65	30	0	5
Río Pánuco, near mouth ¹ ..	6	-	-	-	-	-	-	6	0.00	100 ¹	0	0	0
Pecos R., Texas and N. M.	67	2	13	15	-	1	-	98	0.80	68	31	0	1
Western United States													
Timpie Springs, Utah ²	16	-	35	12	5 ³	-	-	68	1.85	24	69	7 ³	0
Blue Lake, Utah ¹	10	-	-	-	-	-	-	10	0.00	100 ¹	0	0	0
Yaquina Bay, Oregon	23	1	-	-	-	-	-	24	0.04	96	4	0	0
San Francisco Bay	44	-	9	-	3 ³	-	-	56	0.54	79	16	5 ³	0
<i>Lucania interioris</i>													
Ferriño's Canal	16	-	-	-	-	-	-	16	0.00	100	0	0	0
Los Positos	10	-	-	-	-	-	-	10	0.00	100	0	0	0
Marsh's material	16	-	-	-	-	-	-	16	0.00	100	0	0	0
La Angostura Canal	18	-	-	-	-	-	-	18	0.00	100	0	0	0
Río Garabatal	40	-	-	-	-	-	-	40	0.00	100	0	0	0
GRAND TOTALS													
<i>Lucania parva</i> ⁴	494	5	88	84	38	66	3	778	1.20	63	23	5	9
<i>Lucania interioris</i>	100	-	-	-	-	-	-	100	0.00	100	0	0	0

¹ Small size of these specimens no doubt explains the absence of pores.

² The high proportion of specimens with pores in the Timpie Springs population is apparently attributable to their large size and "exuberance."

³ Complete counts of 4 pores were in large specimens only.

⁴ Including one specimen from Irvine Lake, California, with no pores on either side. Its small size (20 mm) may explain in part the poor development of its pores.

TABLE 20
 VARIATION IN NUMBER OF GILL-RAKERS IN *Lucania parva* AND *L. interioris*
 Both sides were usually enumerated. Data graphed in Figure 5

	4	5	6	7	8	9	10	11	12	No.	Mean	SD	2 SE
<i>Lucania parva</i>													
Atlantic Coast													
Southern New England	-	-	-	1	11	26	27	11	1	77	9.51	0.99	0.25
Long Island (Mill Creek) ..	-	-	-	-	2	11	6	1	-	20	9.30	0.71	0.30
Chesapeake Bay	-	1	6	22	15	16	-	-	-	60	7.65	1.03	0.29
Florida													
Florida Keys	-	2	17	10	14	2	2	2	-	49	7.22	1.39	0.43
Bird (Indian) Key	-	1	3	9	13	9	4	1	-	40	8.05	1.27	0.44
Pensacola Bay	-	-	1	15	3	2	-	-	-	21	7.29	0.70	0.33
Coast, Wakulla Co.	-	2	6	13	15	7	1	-	-	44	7.50	1.12	0.37
Juniper Springs Cr.	-	-	7	13	1	1	-	-	-	22	6.82	0.72	0.33
TOTAL FOR FLORIDA	-	5	34	60	46	21	7	3	-	176	7.44	1.22	0.20
Gulf of México													
Lake Pontchartrain, La. ..	-	-	6	7	4	3	-	-	-	20	7.20	1.03	0.50
Texas Coast	-	-	3	13	13	1	-	-	-	30	7.40	0.71	0.28
Río Grande, near mouth ..	1	8	27	19	7	2	1	1	-	66	6.58	1.21	0.33
Río Pánuco, near mouth ..	-	1	3	2	-	-	-	-	-	6	6.17	0.43	0.33
Pecos R., Texas and N. M.	-	2	14	29	32	11	-	-	-	88	7.41	0.97	0.23
Western United States													
Timpie Springs, Utah	1	2	4	13	2	1	1	-	-	24	6.83	1.21	0.54
Blue Lake, Utah	-	-	6	2	-	-	-	-	-	8	6.25	0.43	0.31
Yaquina Bay, Oregon	-	-	1	5	19	14	8	1	-	48	8.54	1.03	0.30
San Francisco Bay	-	-	-	1	13	27	12	1	1	55	9.04	0.87	0.26
<i>Lucania interioris</i>													
Ferriño's Canal	-	-	-	5	2	1	-	-	-	8	7.50	0.71	0.55
Los Positos	-	1	-	1	3	-	-	-	-	5	7.20	1.17	1.14
Marsh's material	-	-	3	6	3	-	-	-	-	12	7.00	0.41	0.26
La Angostura Canal	-	-	1	6	1	-	-	-	-	8	7.00	0.50	0.39
Río Garabatal	-	-	2	12	6	-	-	-	-	20	7.20	0.60	0.25
GRAND TOTALS													
<i>Lucania parva</i> ¹	2	19	104	176	164	133	62	18	2	680	7.81	1.41	0.11
<i>Lucania interioris</i>	-	1	6	30	15	1	-	-	-	53	7.17	0.72	0.22

¹ Including 2 specimens, each with 7 rakers, from Irvine Lake, California.

TABLE 21 (Continued)

	2.5	2.7	2.9	3.1	3.3	3.5	3.7	3.9	4.1	4.3	4.5	4.7	4.9	5.1	5.3	5.5	5.7	5.9	6.1	6.3	6.5	No. Mean
	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.2	4.4	4.6	4.8	5.0	5.2	5.4	5.6	5.8	6.0	6.2	6.4	6.6	
Rio Grande, near mouth	-	-	-	-	1	1	7	2	1	2	-	-	-	-	-	-	-	-	-	-	-	14 3.85
Pecos R., Texas and N. M. ...	-	-	-	-	1	1	3	4	3	1	-	-	-	-	-	-	-	-	-	-	-	16 4.00
Western United States	-	-	-	-	1	4	5	3	-	-	-	-	-	-	-	-	-	-	-	-	-	13 3.70
Timpie Springs, Utah	1	3	8	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	26 3.99
Yaquina Bay, Oregon	-	-	-	-	-	2	4	2	4	-	1	1	-	-	-	-	-	-	-	-	-	17 2.96
San Francisco Bay	-	-	-	1	4	5	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	17 4.02
<i>Lucania interioris</i>	-	-	-	-	1	4	4	2	4	1	-	-	-	-	-	-	-	-	-	-	-	12 3.90
Ferrifo's Canal	-	-	-	-	-	-	-	-	-	-	-	-	2	1	1	-	-	-	-	-	-	5 4.34
Los Positos	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	12 3.50
Marsh's material	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3	-	-	-	16 3.84
La Angostura Canal	-	-	-	-	-	-	-	-	-	-	-	-	2	3	1	1	-	-	-	-	-	3 5.08
Rio Garabatal	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4	2	3	-	-	-	-	5 5.95
GRAND TOTALS	1	5	17	24	36	28	27	16	6	2	-	-	-	-	-	-	-	-	-	-	-	3 5.08
<i>Lucania parva</i> ¹	-	-	2	13	27	42	38	28	23	6	4	-	-	-	-	-	-	-	-	-	-	5 5.95
<i>Lucania interioris</i>	-	-	-	-	-	-	-	-	-	-	-	-	5	7	6	5	-	-	-	-	-	2 5.35
	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	8	10	-	-	-	-	3 5.95
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	8	10	-	-	-	1 5.55
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	9 6.06
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7 5.18
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	2 5.75
	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4	2	3	-	-	-	-	10 5.29
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	10 5.85
	1	5	17	24	36	28	27	16	6	2	-	-	-	-	-	-	-	-	-	-	-	162 3.46
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	183 3.91
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23 5.25
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	29 5.94

¹ Including one measurement of 4.0 for a female from Blue Lake, Utah, and of 4.0 for a male from Irvine Lake, California.

TABLE 22

VARIATION IN BODY DEPTH IN ADULTS AND SUBADULTS OF *Lucania parva* AND *L. interioris*

The figures represent the maximum body depth stepped into the body from tip of snout to end of hypural. Statistical computations derived from uncombined data.

	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.2	4.4	No.	Mean	SD	2 SE
	2.7	2.9	3.1	3.3	3.5	3.7	3.9	4.1	4.3	4.5				
<i>Lucania parva</i>														
Atlantic Coast														
Southern New England	-	-	-	13	19	23	4	-	-	-	59	3.50	0.19	0.05
Long Island (Mill Creek)	-	-	1	5	8	4	-	-	-	-	18	3.41	0.16	0.07
Chesapeake Bay	-	-	2	2	8	30	7	1	-	-	50	3.61	0.17	0.05
North Carolina	-	-	-	-	-	10	9	1	-	-	20	3.77	0.11	0.05
Florida														
Florida Keys	1	13	6	4	1	-	-	-	-	-	25	2.97	0.17	0.07
Bird (Indian) Key	-	5	12	3	-	-	-	-	-	-	20	3.03	0.12	0.05
Bays and keys, W. coast	-	1	2	14	6	3	1	-	-	-	27	3.34	0.19	0.07
Pensacola Bay	-	-	1	7	7	6	-	-	-	-	21	3.42	0.19	0.08
Coast, Wakulla Co.	-	2	9	8	3	-	-	-	-	-	22	3.36	0.16	0.07
Mill Creek, Bradenton	-	-	1	1	11	8	6	1	-	-	28	3.80	0.22	0.08
Slough of St. Johns R.	-	-	-	-	2	4	5	8	6	2	27	3.99	0.27	0.10
Salt Springs Creek	-	-	1	4	16	6	3	3	-	-	33	3.73	0.23	0.08
Juniper Springs Cr.	-	-	-	-	-	13	10	1	3	-	27	3.82	0.36	0.07
TOTAL FOR FLORIDA ¹	1	19	23	39	29	56	30	18	13	2	230	3.53	0.39	0.05
Gulf of México														
Texas Coast	-	-	-	3	10	16	3	-	1	-	33	3.58	0.19	0.07
Río Grande, near mouth	-	-	1	1	9	12	6	-	1	-	30	3.61	0.21	0.08
Río Pánuco, near mouth	-	-	-	-	-	-	-	1	-	-	1	4.00	-	-
Pecos R., Texas and N. M.	-	-	-	1	8	38	8	1	1	1	58	3.68	0.19	0.05
Western United States														
Timpie Springs, Utah ²	-	-	-	9	19	17	3	-	-	-	48	3.51	0.15	0.04
Bluc Lake, Utah ³	-	-	-	-	-	2	2	1	-	-	5	3.82	0.12	0.10
Yaquina Bay, Oregon	-	-	-	2	7	11	-	-	-	-	20	3.54	0.14	0.06
San Francisco Bay	-	-	2	6	13	19	4	-	-	-	44	3.53	0.18	0.06
<i>Lucania interioris</i>														
Ferriño's Canal	-	-	2	-	3	2	1	-	-	-	8	3.43	0.23	0.16
Los Positos	-	-	-	-	3	1	1	-	-	-	5	3.54	0.15	0.13
Marsh's material	-	-	-	4	3	2	1	-	-	-	10	3.45	0.20	0.13
La Angostura Canal	-	-	-	5	4	-	-	-	-	-	9	3.34	0.11	0.07
Río Garabatal	-	-	4	12	3	-	-	-	-	-	19	3.24	0.13	0.06
GRAND TOTALS														
<i>Lucania parva</i> ⁴	1	19	29	81	130	238	76	23	16	4	617	3.56	0.29	0.02
<i>Lucania interioris</i>	-	-	6	21	16	5	3	-	-	-	51	3.36	0.20	0.06

¹ Including one specimen with measurement of 3.9 from Atlantic Beach, Florida, and five, with depth 3.3 to 3.6, from Myakka River, western Florida.

² Mostly large specimens.

³ Mostly small specimens.

⁴ Including one subadult specimen 20 mm long from Irvine Lake, California, with depth 4.5.

TABLE 23

VARIATION IN PROPORTIONAL MEASUREMENT¹ OF PREDORSAL LENGTH IN SUBADULTS AND ADULTS OF *Lucania parva* AND *L. interioris*

	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	No.	Mean
<i>Lucania parva</i>																	
Males	-	-	3	10	18	31	38	24	13	6	2	-	-	-	-	145	52.77
Females	<i>1</i>	-	-	<i>2</i>	<i>10</i>	<i>28</i>	<i>39</i>	<i>44</i>	<i>63</i>	<i>26</i>	<i>18</i>	<i>2</i>	<i>1</i>	-	-	<i>234</i>	<i>54.18</i>
<i>Lucania interioris</i>																	
Males	-	-	-	-	-	-	-	-	-	6	5	6	4	2	-	23	57.61
Females	-	-	-	-	-	-	-	-	-	<i>2</i>	<i>3</i>	<i>6</i>	<i>7</i>	<i>6</i>	<i>2</i>	<i>26</i>	<i>58.69</i>

¹ Measurements are expressed in hundredths of the standard length, segregated by sex. All localities (similar to those utilized for meristics—see Tables 2-20) combined for each species.

TABLE 24

VARIATION IN PROPORTIONAL MEASUREMENT OF DISTANCE FROM ORIGIN OF ANAL FIN TO BASE OF CAUDAL FIN IN *Lucania parva* AND *L. interioris*¹

	31-32	33-34	35-36	37-38	39-40	41-42	43-44	45-46	No.	Mean
<i>Lucania parva</i>										
Atlantic Coast										
Southern New England	-	-	-	1	4	6	1	-	12	40.42
	-	<i>2</i>	<i>16</i>	<i>6</i>	-	-	-	-	<i>24</i>	<i>36.04</i>
Long Island (Mill Creek) ..	-	-	-	-	-	9	-	-	9	41.67
	-	-	<i>4</i>	<i>4</i>	<i>1</i>	-	-	-	<i>9</i>	<i>36.67</i>
Chesapeake Bay	-	-	-	-	4	6	-	-	10	40.70
	-	-	-	<i>7</i>	<i>9</i>	<i>1</i>	-	-	<i>17</i>	<i>38.76</i>
North Carolina	-	-	<i>1</i>	<i>2</i>	<i>6</i>	<i>6</i>	<i>1</i>	-	<i>16</i>	<i>39.81</i>
Florida										
Florida Keys	-	-	-	-	-	7	5	1	13	42.38
	-	-	-	<i>3</i>	<i>7</i>	<i>2</i>	-	-	<i>12</i>	<i>39.42</i>
Bird (Indian) Key	-	-	-	-	1	1	8	-	10	42.80
	-	-	-	<i>4</i>	<i>3</i>	<i>2</i>	<i>1</i>	-	<i>10</i>	<i>39.40</i>
Juniper Springs Cr.	-	-	-	-	-	3	2	-	5	42.20
	-	-	-	-	<i>4</i>	<i>2</i>	-	-	<i>6</i>	<i>40.17</i>
TOTAL FOR FLORIDA	-	-	-	-	1	11	15	1	28	42.50
	-	-	-	<i>7</i>	<i>14</i>	<i>6</i>	<i>1</i>	-	<i>28</i>	<i>39.57</i>

¹ Measurements are expressed in hundredths of the standard length, segregated by sex (figures for males are in **boldface** type; those for females in *italics*). The means were computed from the ungrouped data.

TABLE 24 (Continued)

	31-32	33-34	35-36	37-38	39-40	41-42	43-44	45-46	No.	Mean
Gulf of México										
Alabama (Big Lake)	-	-	-	-	2	4	-	-	6	41.00
Mississippi	-	-	-	-	1	6	5	-	12	42.00
Lake Pontchartrain, La. ..	-	-	-	1	2	-	2	-	5	40.80
Texas Coast	-	-	-	-	2	4	4	-	10	41.70
	-	-	-	1	9	8	1	-	19	40.42
Río Grande, near mouth ..	-	-	-	-	1	2	3	-	6	42.00
	-	-	-	2	4	2	-	-	8	39.00
Río Pánuco, near mouth ..	-	-	-	-	-	1	-	-	1	41.00
Pecos R., Texas and N. M. .	-	-	-	1	3	12	4	1	21	41.67
	-	-	8	14	12	3	-	-	37	37.95
Western United States										
Timpie Springs, Utah	-	-	1	3	10	9	-	-	23	41.96
	-	-	1	14	8	2	-	-	25	38.56
Blue Lake, Utah	-	-	-	-	5	-	-	-	5	39.80
Yaquina Bay, Ore.	-	-	-	7	4	6	3	-	13	41.31
	-	-	-	1	2	4	-	-	7	40.29
San Francisco Bay	-	-	-	-	-	9	3	-	12	41.83
	-	-	1	6	1	7	1	-	16	39.63
<i>Lucania interioris</i>										
Ferrifio's Canal	-	-	-	1	1	1	-	-	3	39.00
	2	2	1	-	-	-	-	-	5	33.40
Los Positos	-	-	-	1	1	-	-	-	2	38.50
	-	-	3	-	-	-	-	-	3	35.67
Marsh's material	2	5	2	-	-	-	-	-	1	35.00
	-	-	-	-	-	-	-	-	9	33.56
La Angostura Canal	-	-	-	3	3	1	-	-	7	38.71
	-	1	1	-	-	-	-	-	2	35.00
Río Garabatal	-	-	-	6	4	-	-	-	10	38.50
	-	-	5	3	1	-	-	-	9	36.67
GRAND TOTALS										
<i>Lucania parva</i> ²	-	-	3	22	75	43	2	145	41.76	
	-	2	31	65	77	49	11	235	38.97	
<i>Lucania interioris</i>	4	8	12	3	1	-	-	28	34.86	

² Including one measurement of 44 for a male from Irvine Lake, California.

TABLE 25
PROPORTIONAL MEASUREMENTS OF *Lucania parva* AND *Lucania interstitialis*¹

	Predorsal Length	Anal Origin to Caudal Base	Body Depth	Caudal-peduncle Depth	Head Length	Head Width	Inter-orbital Width
<i>Lucania parva</i>							
Waquoit Bay, Massachusetts							
5 males, 25-29(26.7)	523-534(528)	394-410(406)	272-303(283)	161-169(165)	304-317(312)	158-167(161)	104-110(107)
5 females, 30-34(31.9)	547-570(558)	355-367(361)	285-324(298)	139-161(148)	297-315(303)	170-187(174)	92-112(103)
Mill Creek, Long Island							
9 males, 25-29(26.5)	519-550(530)	408-424(418)	277-297(286)	157-174(163)	300-320(308)	150-161(154)	104-112(108)
9 females, 30-35(33.4)	542-569(555)	352-389(366)	301-327(314)	140-156(147)	286-315(303)	156-172(165)	100-109(106)
Coast, Wakulla Co., Florida							
15 males, 26-29(27.5)	-	-	255-303(285)	154-177(165)	298-335(312)	160-180(169)	-
10 females, 31-33(32.3)	-	-	278-306(289)	152-174(164)	280-296(289)	151-168(155)	-
Juniper Springs Cr., Florida							
5 males, 26-28(26.8)	496-519(507)	413-434(425)	257-285(274)	153-163(158)	316-330(325)	165-175(170)	124-130(126)
6 females, 27-33(29.8)	509-535(523)	391-410(401)	258-280(270)	137-155(145)	307-324(318)	164-178(171)	113-125(120)
Texas Coast							
4 males, 21-27(25.5)	521-556(538)	395-413(405)	251-313(287)	144-178(163)	301-334(316)	149-194(168)	99-105(103)
Río Pánuco, near mouth							
1 female, 19.7	527	402	257	150	314	164	97
Pecos R., Texas and N. M.							
7 males, 20-30(24.1)	515-547(533)	387-419(410)	260-286(272)	147-159(153)	298-315(308)	151-161(156)	97-110(103)
12 females, 21-34(29.6)	528-563(543)	357-409(381)	259-279(269)	132-159(144)	263-307(295)	147-161(155)	90-103(97)
Timpie Springs, Utah							
6 males, 27-31(29.3)	505-529(516)	407-445(433)	285-310(296)	164-176(168)	291-327(309)	137-163(153)	103-115(109)
6 females, 33-44(37.8)	532-560(549)	366-399(386)	259-307(287)	133-160(149)	283-301(293)	145-165(156)	103-112(107)
San Francisco Bay, Calif.							
12 males, 24-29(26.6)	503-546(529)	407-430(419)	273-302(286)	158-182(167)	291-332(311)	153-174(166)	106-121(113)
16 females, 25-39(31.4)	511-573(543)	364-425(396)	268-339(303)	146-171(157)	290-327(307)	153-193(173)	102-120(110)

¹ Measurements, in mm., made in accordance with the methods outlined by Hubbs and Lagler (1958), are expressed in thousandths of the standard length. Ranges are given, with averages, in parentheses, in **boldface** type for males and in *italics* for females (of stated standard lengths).

TABLE 25 (Continued)

	Predorsal Length	Anal Origin to Caudal Base	Body Depth	Caudal-peduncle Depth	Head Length	Head Width	Inter-orbital Width
<i>Lucania interioris</i>							
Ferreño's Canal							
3 males, 23-29(26.0)	558-576(568)	372-407(389)	274-304(291)	166-174(171)	319-324(322)	175-181(179)	113-119(117)
5 females, 27-31(29.6)	564-599(584)	320-358(333)	262-324(297)	145-163(154)	300-320(311)	172-194(181)	104-123(114)
Los Positos							
2 males, 21-25(23.3)	570-570(570)	384-393(389)	279-292(286)	162-173(167)	315-329(322)	177-182(179)	115-115(115)
3 females, 19-25(22.6)	576-596(585)	346-363(356)	271-292(285)	157-164(161)	327-333(330)	175-181(179)	114-116(115)
Marsh's material							
1 male, 15.8	591	349	295	175	367	206	125
8 females, 15-26(22.6)	557-601(581)	309-359(335)	268-299(284)	152-177(167)	345-375(364)	193-212(203)	112-129(119)
La Angostura Canal							
Holotype, male, 26.5	587	391	307	183	311	173	118
7 males, 18-26.5(22.7)	563-592(580)	373-405(388)	295-317(305)	168-190(181)	311-332(320)	173-187(179)	113-119(116)
2 females, 22-22(22.1)	589-610(599)	344-362(353)	306-307(307)	178-179(179)	315-320(317)	187-191(189)	121-122(121)
Rio Garabatal							
5 males, 21-25(22.5)	558-577(567)	378-394(384)	301-324(312)	175-181(177)	323-330(326)	181-193(188)	120-131(126)
5 females, 24-27(25.6)	563-609(592)	348-383(360)	304-342(321)	165-177(170)	310-330(322)	175-207(188)	115-125(121)
<i>Lucania parva</i>							
Waquoit Bay, Massachusetts							
5 males, 25-29(26.7)	73-82(79)	97-99(96)	313-351(335)	229-264(245)	241-265(250)	172-189(182)	152-178(167)
5 females, 30-34(31.9)	74-80(77)	87-98(91)	277-281(279)	204-217(208)	216-238(236)	147-162(155)	126-143(131)
Mill Creek, Long Island							
9 males, 25-29(26.5)	75-86(81)	94-103(99)	332-376(347)	243-269(255)	236-256(246)	178-205(191)	137-177(157)
9 females, 30-35(33.4)	79-88(83)	84-93(89)	263-302(280)	194-210(202)	222-240(231)	164-184(175)	116-137(126)
Coast, Wakuulla Co., Florida							
15 males, 26-29(27.5)	-	96-109(102)	-	-	-	191-213(202)	127-164(146)
10 females, 31-33(32.3)	-	97-105(101)	-	-	-	177-206(195)	137-157(146)

TABLE 25 (Continued)

	Snout Length	Orbit Length	Dorsal Fin Length	Anal Fin Length	Longest Caudal Ray	Longest Pectoral Ray	Pelvic Fin Length
Juniper Springs Cr., Florida							
5 males, 26-28(26.8)	87-94(90)	99-109(102)	300-329(317)	225-244(238)	238-249(243)	197-221(212)	141-153(150)
6 females, 27-33(29.8)	91-99(95)	91-105(99)	287-310(293)	211-234(222)	236-254(242)	176-215(196)	140-153(145)
Texas Coast							
4 males, 21-27(25.5)	78-87(82)	98-102(100)	284-339(313)	220-268(239)	273-298(281)	179-201(193)	128-151(139)
Río Pánuco, near mouth							
1 female, 19.7	78	112	273	211	257	199	137
Pecos R., Texas and N. M.							
7 males, 20-30(24.1)	70-82(77)	99-112(105)	277-344(307)	227-257(244)	244-282(268)	168-201(186)	135-152(146)
12 females, 21-34(29.6)	72-81(76)	88-107(97)	270-306(282)	212-238(224)	229-313(263)	166-208(184)	121-153(134)
Timpie Springs, Utah							
6 males, 27-31(29.3)	78-84(82)	98-101(99)	345-366(359)	260-280(266)	226-261(250)	184-200(191)	164-196(177)
6 females, 33-44(37.8)	79-85(82)	80-90(85)	271-292(284)	196-216(206)	209-252(230)	158-184(173)	129-148(139)
San Francisco Bay, Calif.							
12 males, 24-29(26.6)	78-90(84)	90-103(97)	276-352(305)	208-257(228)	252-280(266)	188-221(204)	131-161(148)
16 females, 25-39(31.4)	76-90(82)	86-102(91)	271-305(287)	181-228(211)	221-275(252)	170-204(187)	127-150(140)
<i>Lucania interioris</i>							
Ferrigno's Canal							
3 males, 23-29(26.0)	85-90(88)	92-100(96)	289-317(306)	233-251(241)	194-235(216)	171-185(180)	105-115(111)
5 females, 27-31(29.6)	83-92(86)	85-95(89)	244-283(258)	181-217(202)	189-232(206)	151-169(163)	92-114(99)
Los Positos							
2 males, 21-25(23.3)	82-84(83)	107-112(109)	273-285(279)	209-225(217)	217-222(219)	195(im 1)	105-107(106)
3 females, 19-25(22.6)	82-89(86)	99-105(102)	265-275(270)	194-211(205)	208-215(212)	179-181(180)	101-106(104)
Marsh's material							
1 male, 15.8	97	118	273	237	239	195	93
8 females, 15-26(22.6)	86-101(92)	102-123(108)	234-272(252)	198-219(211)	206-251(218)	168-194(175)	84-100(95)
La Angostura Canal							
Holotype, male, 26.5	83	92	294	243	217	187	115
7 males, 18-26.5(22.7)	78-91(85)	92-108(99)	285-302(295)	235-259(245)	217-268(235)	177-203(192)	109-124(115)
2 females, 22-22(22.1)	81-86(83)	94-97(95)	267-272(269)	218-235(227)	219-248(233)	188-188(188)	105-106(105)
Río Garabatal							
5 males, 21-25(22.5)	85-92(89)	100-103(101)	271-319(286)	205-247(230)	212-233(223)	-	104-112(107)
5 females, 24-27(25.6)	84-88(86)	90-110(100)	260-296(272)	199-236(212)	215-224(219)	-	99-104(101)

TABLE 26

MORE SIGNIFICANT CHARACTERS AND RELATIONS OF THE PECOS RIVER RACE OF *Lucania parva*
Disregarding the diverse races of Florida

Character	Table	Figure	Mode	Mean	Remarks
Dorsal rays	2	2	11	10.80	Averaging slightly lower than along Gulf of México Coast and over most of range of species.
Anal Rays	4	2	9	9.26	As in far north and in coastal Florida, but averaging even lower; about same as in Chesapeake Bay.
Scales					
Dorsal to anal	12	-	8 (9 close)	8.62	Lowest for the species; mode 9 or 10 in all other locations, with lowest other mean 8.90.
Around body	13	5	21	21.06	Low, as also along Gulf of México Coast, much lower than in far north.
Around peduncle	14	-	14-15	14.42	Much lower than in far north; reduction to 12 much less common than along Gulf of México Coast.
Vertebrae	15	-	28	27.96	About as in far north and in Lake Pontchartrain; averaging fewer than in coastal Texas (mean, 28.24).
Preopercular pores	16	7	7 (8 close)	7.34	Resembles only the far-northern races in frequency of counts higher than 7.
Supraorbital pores	17	7	7 (8 close)	7.63	Often increased beyond 7, as in the far north, instead of being rarely increased and not beyond 8 (other localities); but unlike far-northern stocks in not having number reduced below the mode at 7.
Lachrymal pores	18	7	0	2.13	Higher indicated percentage (43) with no pores than in Gulf coastal samples; similar in this respect to far-northern types, but differing from them in the unique high incidence of 5 pores.
Mandibular pores	19	7	0	0.80	Rather like most other races; differing from the southern New England race in frequently having some mandibular pores.
Gill rakers	20	5	8 (7 close)	7.41	Essentially like Gulf Coast form, much lower than in far north.
Pelvic-fin length	21	-	{ 3.7-3.8 3.9-4.0	3.70 3.99	Not very distinctive; sexual dimorphism slight (probably due to environment).
Anal-to-caudal distance ..	24	-	{ 42 39	41.67 37.95	Females, shorter than along Gulf of México Coast, but longer than in far north; males less distinctive.
(% standard length) ¹					
Body depth	22	-	3.6-3.7	3.68	Much as in Gulf Coast and Middle Atlantic Coast forms; less than in far north.
(into standard length)					

¹ Data for males and females given separately, in that order.

TABLE 27

COMPARISON OF *Lucania interioris* WITH *Lucania parva*

These species are further compared with one another and with two other species in Table 1

Character	<i>Lucania interioris</i>	<i>Lucania parva</i>
Length of pelvic fin stepped into predorsal length (Table 21)	Males: 4.9–5.6 (ave., 5.25) Females: 5.4–6.5 (ave., 5.94)	Males: 2.5–4.4 (ave., 3.46) Females: 3.2–4.8 (ave., 3.91)
Greatest width of head in relation to length of snout plus eye	Somewhat greater	Definitely less
Depth of caudal peduncle (Table 25)	About 2.0 in greatest body depth; about half to two-fifths distance from anal origin to caudal base	About 3.0 in greatest body depth; about one-third distance from anal origin to caudal base ¹
Position of dorsal fin and of anus (Tables 23 and 24)	More posterior (each with slight overlap)	Predorsal length greater; urosome longer ²
Dorsal fin of male, in life	Chalky blue, without yellow or orange	Dusky, tinged with yellow on membranes; orange-red or brick-red on posterior corner
Anal and pelvic fins in live adult males	Deep blue to turquoise	Orange or brick-red, at least in a submarginal band on anal
Pigmentation of dorsal fin in mature males	General surface more darkened	Less darkened
Pigmentation of anal fin in mature males	Blackish border lacking; membranes blackened	Blackish border developed; membranes paler
Fine black streak along mid-ventral edge of caudal peduncle	Undeveloped	Weakly to strongly developed
Pair of dark streaks on top of muzzle (on either side of midline)	Short, typically parenthesis-like, not continued backward	Longer, straighter, typically subparallel and more or less definitely extended backward between eyes
Black pigment on cheek	Largely confined to border of eye; not forming a subocular bar	More extensively developed, forming a more or less definite subocular bar extending downward and forward
Caudal fin of male	Darker toward margin but without a definite blackish band	Definitely margined by a blackish band
Blackish outer border of pelvic fin	Broader and more diffuse	Narrower and sharper
Dark bordering of scale pockets	Less boldly set off from pale centers; less sharply marked	Bolder and sharper; dark borders conspicuous and regular; melanophores often in single file

¹ In the deeper-bodied form of western Florida, becoming most extreme in the Florida Keys, the caudal peduncle may be almost half as long as the anal-caudal distance, but remains much less than one-half the body depth.

² Except in northernmost race.

TABLE 27 (Continued)

Character	<i>Lucania interioris</i>	<i>Lucania parva</i>
Squarish lateral dusky blotches	Not discernible	Often more or less conspicuous, especially in freshwater forms
Supraorbital pores (Table 17; Fig. 7)	Almost always fewer than 5	Almost always more than 5 (except in far north)
Lachrymal pores (Table 18; Fig. 7)	Almost invariably absent	Often to always 1-4
Mandibular pores (Table 19; Fig. 7)	Invariably absent	Often developed (except rarely in far north)
Pectoral-ray counts (Table 8; Fig. 4)	Averaging more	Averaging fewer
General body form	Decidedly more oblong, less rhombic, with subparallel dorsal and ventral contours between isthmus and anus	Less oblong, more rhombic
Length of head (Table 25)	Usually greater	Usually less
Fins	Generally smaller and more rounded	Generally larger and less rounded
Dorsal and anal rays (Tables 2 and 4; Fig. 2)	Dorsal rays averaging fewer; regression of anal-ray counts on dorsal-ray counts very steep (Fig. 3)	Dorsal rays averaging more; regression line of moderate slope (Fig. 3)

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PLATE I

Diverse form and coloration of *Lucania parva* in different parts of Florida

All to the same scale. Males in upper half, females below. Left column: males from mangrove channel in Shell Key (UMMZ B61-64); females from bay in Crawl Key (UMMZ B61-46). Center column: Juniper Springs Creek (UMMZ 110672). Right column: Pensacola Bay (UMMZ 136550). Photo by Scripps Institution of Oceanography.

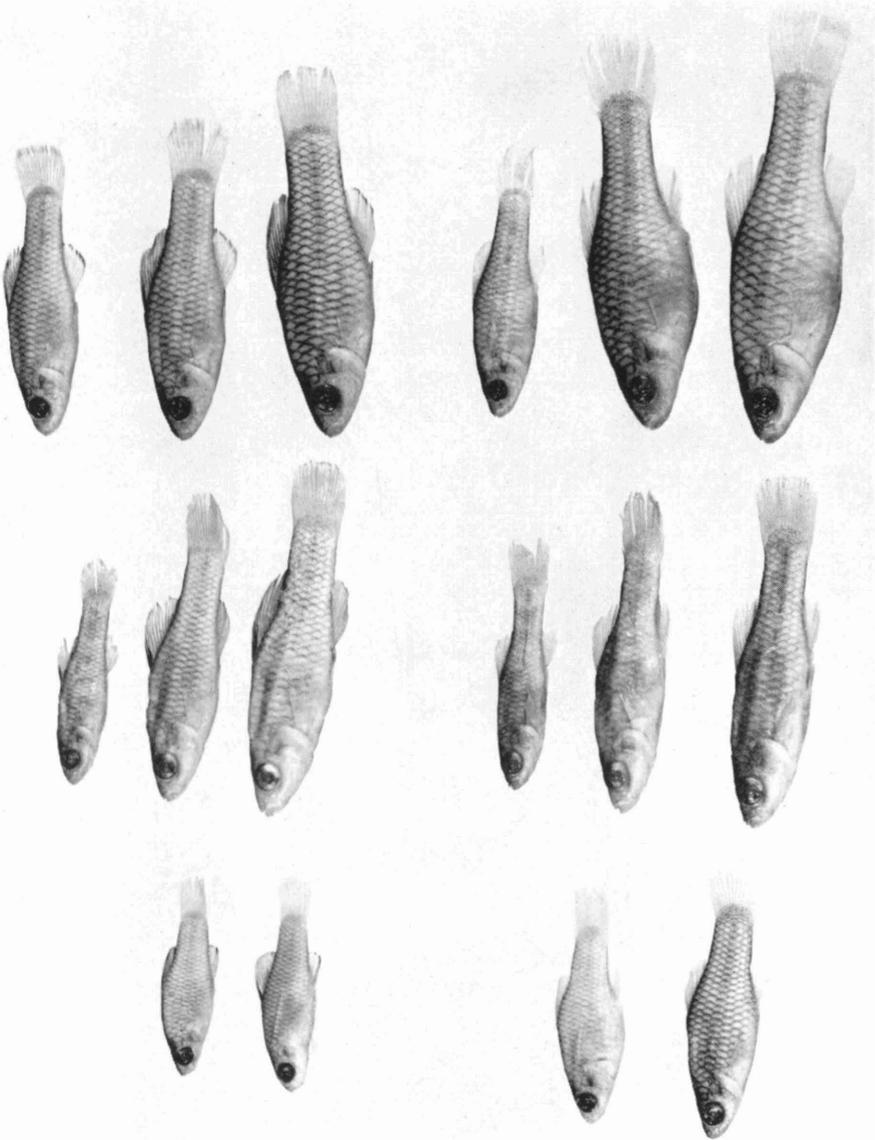


PLATE II

Comparison between samples of *Lucania parva* from Pecos River, Texas (left), and from Timpie Springs, Utah (right), to show exuberance after introduction of Pecos stock into Utah.

Left: top, UMMZ 170118, male 23.2 mm long, from below U. S. 90 highway bridge, Val Verde County, Texas; middle, female 31.6 mm, from same locality; bottom, UMMZ 179914, female 40.5 mm, from below U. S. 67 highway bridge, Pecos and Crockett counties, Texas. Right: top, male 27.4 mm; middle, male 29.0 mm; and bottom, female 40.5 mm—all from UMMZ 178651, Timpie Springs, Tooele County, Utah. Photo by Scripps Institution of Oceanography.

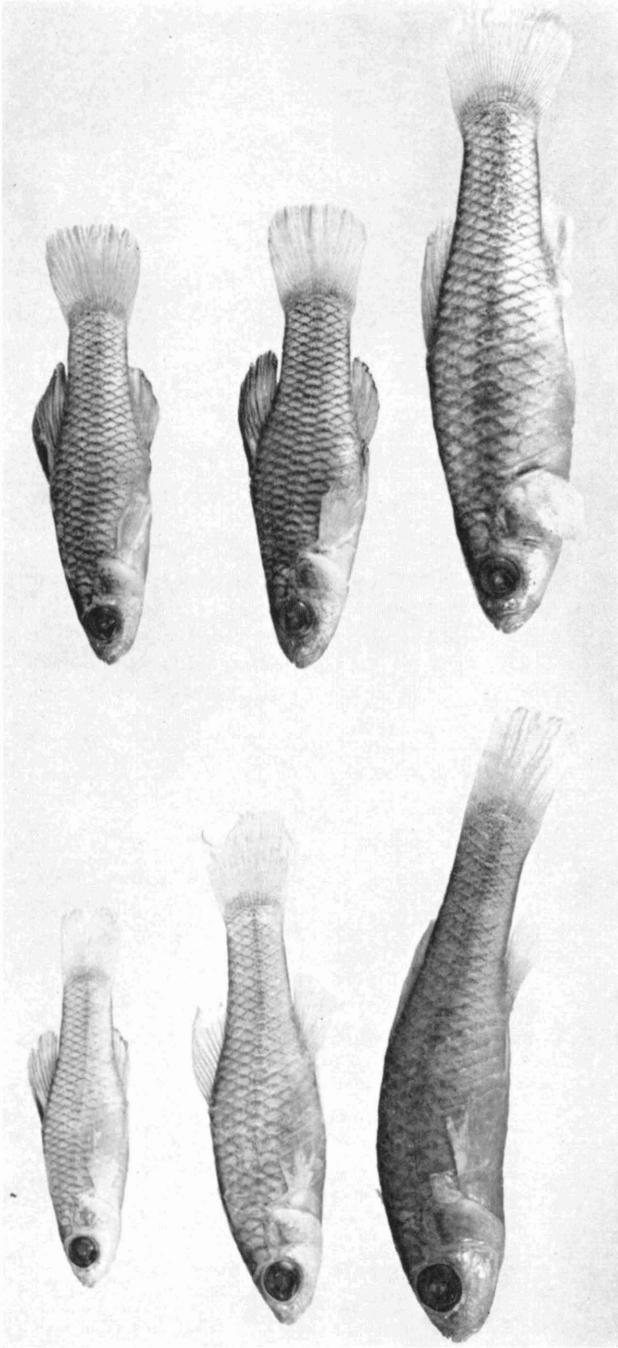
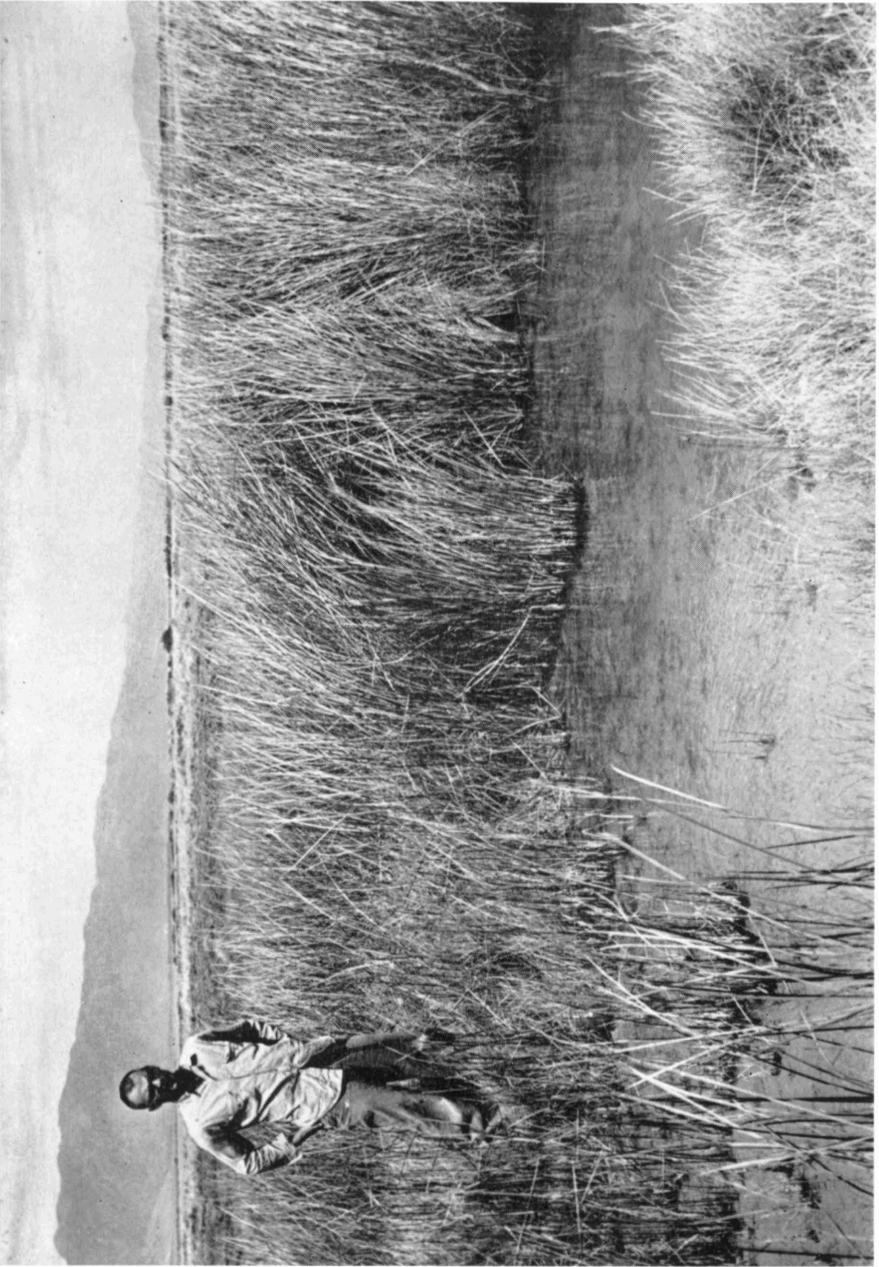


PLATE III

Habitat of *Lucania interioris*, and general view of the Cuatro Ciénegas Basin, to which it is restricted.

Marshy pool in meadow along the eastern side of Río Garabatal, near source of La Angostura Canal (location 1 on insert in Fig. 1); about 8 km west-northwest from tip of San Marcos Mountain. The view is eastward, across most of the interior-drainage part of the floor of the basin, toward the outlet gap at the northeast corner. The village of Cuatro Ciénegas lies near the base of the mountains (in left-distance). The largest series of paratypes came from this one shallow pool. From Kodachrome taken by Miller on April 8, 1961.



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