A SYSTEMATIC STUDY OF ETHEOSTOMA LONGIMANUM AND ETHEOSTOMA PODOSTEMONE (PISCES, PERCIDAE)

by

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Thesis submitted to the Graduate Faculty
of the Virginia Polytechnic Institute
in candidacy for the degree of

MASTER OF SCIENCE

in

Zoology

September, 1964
Blacksburg, Virginia

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ACKNOWLEDGMENTS

The writer wishes to express his appreciation to Dr. Robert D. Ross, at whose suggestion this study was begun, and whose help and guidance were largely responsible for its completion. I am also indebted to Dr. Perry C. Holt and Dr. Stuart E. Neff, members of my graduate committee, and to the following graduate students at V. P. I. who aided in collecting specimens for study: Charles Heartwell, Edgar McConnell, Paul Buhan, Robert Jenkins, and Joe Roles.

INTRODUCTION AND LITERATURE REVIEW

The Percidae are an important group of fresh-water fishes in the Northern Hemisphere. Berg (1947: 474) reported fossil percids from Eocene deposits in Europe and North America, but little is known of the evolutionary history of the family. Various authors (Jordan and Eigenmann, 1890: 330; Henry, 1962: 430; Collette, 1963: 620) have pointed out morphological and anatomical similarities between the Percidae and the Serranidae, and it is to the anadromous and fresh-water members of this group that the perches seem most closely related.

The Percidae were formerly considered as being divided into two subfamilies, the Percinae, composed of Perca, Stizostedion, and other European genera, and the Etheostomatinae, composed of the various genera of darters restricted to North America. However, Collette (1963), chiefly on the size and development of the anteriormost interhaemal bone and anal spines, divided the Percidae into the two subfamilies Percinae (Perca, related genera, and American darters) and Luciopercinae (Stizostedion and related genera).

Bailey (in Bailey, Winn, and Smith, 1954: 139-141) recognized three primary natural groups within the subfamily Etheostomatinae (tribe Etheostomatini of Collette). He considered as most specialized those species with modified midventral scales and placed eight such former genera into the single genus, Percina. The second group was characterized by "the naked midline of the belly and the single weak anal spine." In this group Bailey placed the genera Ammocrypta and Crystallaria, the sand darters. All the remaining darters were placed in the genus Etheostoma.

Bailey's reason for placing many groups formerly given generic rank into a single genus "consists in evidence that the characters employed to define and delimit the groups are highly variable both intraspecifically and interspecifically, are subject to complete overlap from group to group, and are commonly the product of convergent evolution." Bailey (in Bailey and Gosline, 1955: fig. 1) recognized essentially the same generic classification as he had in Bailey, Winn, and Smith (1954). These were *Percina* (20 species), *Ammocrypta*, which included the former monotypic genus *Crystallaria* (5 species), and *Etheostoma* (presently over 70 species). He also recognized many former generic names as subgenera; *Etheostoma* being composed of 12 subgenera, the most generalized of which are *Boleosoma* and *Etheostoma*. In Table I (p. 15), Bailey listed seven species within *Boleosoma*: *Etheostoma nigrum* (3 subspecies), *E. perlongum*, *E. chlorosomum*, *E. jessiae*, *E. stigmaeum*, *E. longimanum*, and *E. podostemone*. Cole (1957: 3-4) recognized 3 species groups of *Boleosoma* in the eastern United States east of the Appalachian Mountains. These were: (1) *Etheostoma nigrum* complex composed of five subspecies and characterized by small size, typically 9 preoperculomandibular pores, and incomplete infraorbital canal. (2) *Etheostoma olmstedi* complex composed of four subspecies plus *E. perlongum*, an endemic form of Lake Waccamaw, North Carolina, and characterized by larger size, typically 11 preoperculomandibular pores and complete infraorbital canal. (3) *Etheostoma longimanum* - *E. podostemone* group, endemic to the James and Roanoke River systems respectively. The three other species, *E. jessiae*, *E. chlorosomum*, and *E. stigmaeum*, occur in the Mississippi and Gulf Coast drainages.

E. longimanum was first described by Jordan (1889a). In a later paper published the same year (1889b), he gave the original description of *E. podostemone* as well as another description of *E. longimanum* from better material. Jordan stated that *E. podostemone* was allied to *E. longimanum*, and differed chiefly in the larger scales and smaller mouth. Cockerell and Elder (1914) studied the scales of *E. nigrum*, *E. olmstedi* and *E. podostemone* and found characters to distinguish the three. Raney and Lachner (1943) reported on the age and growth of *E. nigrum olmstedi* and *E. longimanum*. They found both to be short lived species, with males having a faster growth rate than females during the second year of growth. Moore (1957: 184) separated *E. podostemone* from *E. longimanum* primarily on differences in snout profile. Eddy (1957: 209-210) used the ratio of snout length to eye diameter as the major differentiating character between the two. Cole (1957) stated that *E. longimanum* and *E. podostemone* were not closely related to either *E. olmstedi* or *E. nigrum*, and are characterized by a complete infraorbital canal and two anal spines. He presented data on several characters which serve to separate *E. longimanum* from *E. podostemone*, but for many of these characters he examined only 5 or 10 individuals.

The available information thus appears, and has proven to be, inadequate for separating the two species, and casts doubt upon the present taxonomic status of both. The objective of this paper is to study the systematics of *Etheostoma longimanum* and *Etheostoma podostemone*, to re-evaluate their taxonomic status, and to study their distribution and relationships.

METHODS

The following counts were made following the standards of Hubbs and Lagler (1947: 9-12):

Scales in lateral line.

Scale rows above lateral line to origin of first dorsal fin.

Scale rows above lateral line to origin of second dorsal fin.

Scale rows below lateral line to origin of anal fin.

Scale rows around caudal peduncle.

Spines in first dorsal fin.

Rays in second dorsal fin.

Rays in anal fin.

Rays in right and left pectoral fin.

In addition, the following two counts were made:

Lateral scale rows from origin of first dorsal fin to origin of second dorsal fin.

The summation of: scales around caudal peduncle; scales above lateral line to origin of second dorsal fin; scales below lateral line to origin of anal fin.

The following measurements were taken to the nearest tenth of a millimeter with the use of dial calipers and were made following the standards of Hubbs and Lagler (1947: 13-15): standard length, greatest body depth, caudal peduncle depth, head depth, head length, snout length, postorbital length of head, length of longest pectoral ray, length of longest pelvic ray, length of first dorsal fin base, length of depressed second dorsal fin, caudal peduncle length, predorsal length, length of orbit, length of lower jaw (to end of maxillary).

Various workers (Hubbs and Cannon, 1935; Cole, 1957; Collette and Yerger, 1962; Collette, 1962) have found the condition of the cephalic canals to be of systematic importance in the Etheostomatinae. These canals were examined in _E_. _longimanum_ and _E_. _podostemone_, and their arrangement and condition are given in the description of each species. The terminology used follows that of Hubbs and Cannon (1935: 10), with the exception that preoperculomandibular is used in place of the operculomandibular of Hubbs and Cannon. Counts were also made for the number of pores opening from the preoperculomandibular and infraorbital canals.

Only individuals 30 mm or greater in standard length were examined in this study, with all bilateral counts and measurements being made on the left side. For comparative purposes, all measurements except lower jaw length and orbit length were converted to per cent of standard length. Lower jaw length and orbit length were converted to per cent of head length. Snout length was converted to per cent of head length as well as per cent of standard length.

The sex of all individuals examined was determined by differences in the genital papillae of males and females. At the beginning of the study these differences were verified by dissection and examination of the gonads.

Frequency distributions of all counts and proportional measurements are presented in Tables 1-29. The arithmetic mean ($\bar{x}$), standard deviation (s), and standard error of the arithmetic mean (s_M) were calculated for each species by formulae given by Simpson and Roe (1939: 87, 115, 154).

To check for sexual dimorphism, the arithmetic means of all proportional measurements were calculated separately for males and females. No significant differences were found to exist between sexes of the same species for any measurement except the length of the depressed second dorsal fin. This measurement shows definite sexual dimorphism, and is presented in separate frequency distributions (Table 24 and Figs. 24 and 30) for each sex. All other frequency distributions represent combined data for males and females of the same species.

The two species were compared following Ginsberg's (1938: 260-261) arithmetic definition of species, subspecies, and race. In this, frequency distribution curves (Figs. 1-29 pp. 94-122) were constructed for each character examined. For any given character, an average overlap of the two curves of 10 per cent or less was considered to be a specific differentiation for that particular character. An average overlap of 15 to 25 per cent was a subspecific difference, and from 30 to 40 per cent a racial difference. An average overlap of more than 40 per cent indicated a subracial difference, and the two populations were called varieties. In contrast to Ginsberg's use of the single most divergent character as an indication of degree of differentiation, as many seemingly important morphological characters were examined as was possible.

Sample comparison diagrams developed by Hubbs and Perlmutter (1942: 582-592) and Hubbs and Hubbs (1953: 49-56) are given in Figs. 31-34, pp. 124-127. and serve as a graphical analysis of the significance of differences between the two species. In these diagrams, the horizontal line represents the range, the vertical line at right angles to the range represents the mean, the colorless rectangle represents one standard deviation on either side of the mean, and the black rectangle two standard errors on each side of the mean. When the colorless rectangles neither touch or overlap, a specific level of differentiation usually exists between the two populations for this particular character. When the colorless rectangles touch or overlap, but the black rectangles do not touch, a subspecific level of differentiation usually exists. An overlap of one-third or less between the black rectangles usually indicates a subracial level of differentiation, or both samples may well have come from the same place. However, an overlap of greater than 33 per cent between these rectangles usually indicates that no reliance can be placed on the significance of difference between the two populations.

MATERIALS

Materials used in this study are listed under the name of the stream in which they were collected on pp. 30-32 for _E_. _longimanum_ and pp. 41-45 for _E_. _podostemone_. Collection localities are plotted as solid black circles on Figs. 35 and 36, pp. 128-129. All collections are deposited in the Virginia Polytechnic Institute Fish Collection and are catalogued under the collection numbers given.

ETHEOSTOMA LONGIMANUM

Synonymy

Etheostoma longimana - Jordan, 1889a: 179 (original description; type MCZ 24619; James River, Virginia; subgenus Imostoma).

Etheostoma longimane - Jordan, 1889b: 361-362 (description from better material; "A.I,8" probably in error; locality records). Jordan, 1890: 112 (locality records; habitat notes). Jordan, 1916: 126 (description; range).

Boleosoma longimanus - Jordan and Evermann, 1896a: 1054-5 (synonymy; description; "A.I,8" probably copied from Jordan 1889b, in error). Cockerell, 1914: 155 (locality record). Jordan, 1916: 356 (appendix changes text name from Etheostoma longimane). Fowler, 1918: 18 (locality record).

Etheostoma longimanus - Fowler, 1923: 10-11 (locality record; disagreed with Jordan and Evermann on distinguishing features between E. longimanum, E. podostemone, and E. nigrum.

Ulocentra longimane - Jordan, 1929: 158 (description; range).

Imostoma longimane - Jordan, Evermann, and Clark, 1930: 286 (synonymy; range).

Ulocentra longimana - Pratt, 1935: 121 (description; range).

Boleosoma longimanum - Raney and Lachner, 1943: 229-238 (age and growth studies). Burton and Odum, 1945: 186, Table IV (locality records); 191, Table VI (Johns Creek); 192 (range). Raney and Lachner, 1946a: 675 (found frequently with Thoburnia rhothoeca). Raney, 1950, 176-177 (range; questioned Fowler's (1945: 37) record of Cottogaster podostemone from

James and C. longimanus from Potomac); 188 (in list of fishes common in the mountain area). Lachner, Westlake, and Handwerk, 1950: 99 (refers to age and growth studies by Raney and Lachner (1943).

Cottogaster longimanus - Fowler, 1945: 37 (range, Potomac in error); 84 (synonymy; locality records); fig. 16.

Etheostoma longimanum - Fahy, 1954: 153, 188 (referred to age and growth studies by Raney and Lachner); 199 (growth comparison of male to female). Bailey and Gosline, 1955: 15 (subgenus Boleosoma; vertebral counts); 38 (locality records). Cole, 1957: 210-212 (synonymy); 213 (range); 213-215 (diagnosis); 215-216 (locality records). Eddy, 1957: 210 (brief description; range). Moore, 1957: 184 (key); 189-190 (brief description; range). Speare, 1960: 241 (referred to Raney and Lachner, 1943). Gilbert, 1961: 445 (endemic of James); 456 (possible evolutionary history).

Types

In his original description, Jordan (1889: 179) designated as types eight specimens "taken by Professor Baird about 1855, in a tributary of the James River, Virginia," and catalogued as MCZ 24619. Cole (1957: 212-213) reported that three of these types were later transferred to the U. S. National Museum and recatalogued as USNM 120258. He also stated that these three specimens were examined by Lachner in 1946 and identified as two E. longimanum, and one specimen identified by Cole as E. nigrum jamesense. Cole reexamined the types of E. longimanum in 1956 and designated as the lectotype of E. longimanum: "USNM 120258, an adult, sex unknown, 44 mm in standard length. The other specimen of longimanum, an adult, sex unknown, 42 mm in standard length." Cole also reported that the types were very soft and fragile. Due to the fragile condition of these individuals and their recent reexamination, they were not examined by the writer during the course of this study.

Range

Etheostoma longimanum is endemic to the James River system in Virginia and West Virginia. Its distribution within this system is shown on Fig. 36, p.129, from data found in the literature and the V. P. I. collection records. Raney (1950: 188) listed E. longimanum as common in the mountain region, but (p. 189) did not list it as one of the species found in both the upper Piedmont and mountainous region. His use of the term "mountainous region" refers only to fish distribution, and (p. 187) he defined this region as extending from the Allegheny Mountains as far east as Lynchburg and Charlottesville, Virginia. From Fig. 36, it can be seen that the present known distribution of E. longimanum within the James River system appears to be limited to mountainous streams of the Allegheny - Blue Ridge Mountain area and to mountainous tributaries and headwaters of Piedmont streams. This general area coincides with Raney's "mountain region."

Habitat

Jordan (1889b: 361) reported that E. longimanum "abounded in rocky, swift waters, especially among river weeds," and in 1890 (112) he stated that E. longimanum was "very abundant in the tributaries of the upper James especially in weedy places where the current is swift." In various collections taken by the writer, E. longimanum was fairly abundant in the small to medium sized tributaries of the upper James, and was usually found in the deeper riffles of from 6 inches to 2 feet in depth with a moderate to moderately fast current. It is especially abundant in those riffles which contain fairly large flat rocks lying rather loosely on each other and situated in such a manner as to provide space beneath them. It appears that E. longimanum spends most of its time underneath such rocks, emerging primarily to feed.

Description

The body of E. longimanum is moderately elongate and little compressed, with greatest body depth 16.8-20.7% ($\bar{x}$: 18.6%) of standard length and caudal peduncle depth 8.8-11.2% ($\bar{x}$: 10.3%) of standard length. The largest male examined was 73.5 mm SL and the largest female 66.2 mm. Head length is moderate, $\bar{x}$: 24.5% in standard length. The snout is somewhat blunt, with the profile gently sloping from the eyes and becoming almost vertical anterior to the anterior nostrils; length most often is greater than the diameter of the orbit. The premaxillaries are protractile and the maxillaries reach to or posterior to the front of the eye. The mouth is small, horizontal, and slightly subterminal, with teeth being present on the premaxillae, vomer, palatines, and dentary. The gill membranes are rather broadly connected and there are 6 branchiostegal rays. The preopercle is entire.

In the lateral-line system of the head, the lateral canal opens in five pores, as is typical of all darters (Raney and Hubbs, 1948:17; Hubbs and Cannon, 1935:10). The supratemporal canal is complete and opens typically in a median and two lateral pores. Occasionally a forth or fifth pore is present between the median and two lateral pores, but this does not represent a break in the canal. The anterior nasal pore of the supraorbital canal opens before and on line with the anaterior nostril. The posterior nasal pore opens just anterior to and above the posterior nostril. The interorbital pore varies somewhat in position, but is always anterior to the narrowest part of the interorbital region. The coronal pore was present in all E. longimanum examined, and always opened anterior to the posterior margin of the eye and anterior to the postorbital pores. The postorbital pore opens posterior to the orbit and about mid-way between the dorsal edge of the orbit and the junction of the supraorbital and infraorbital canals. The infraorbital canal is complete and opens in from 7 to 9, usually 8 pores. This canal runs along the ventral edge of the orbit and terminates in a pore located just ventral to the anterior nostril and about mid-way between the anterior nostril and the orbit. Posterior to this pore two rather long conspicuous tubes extend ventrally and anteriorly from the infraorbital canal, each opening in a pore on the fleshy edge of the upper lip; one just anterior to the terminal pore and the other on line with the posterior edge of the premaxillae. The five remaining pores are located posteriorly at fairly even intervals, and connect with the canal by short tubes. The preoperculomandibular canal is complete and opens in 9 to 11, usually 10 pores. This canal, as is true in most, if not all, darters (Hubbs and Cannon, 1935: 10), is not connected to the lateral canal. It originates in a pore just above the posterior dorsal edge of the preopercle, runs along its posterior edge ventrally and anteriorly giving off 5 pores, and onto the lower jaw where it usually opens in four pores.

The cheeks, nape, breast, and anterior half of the belly are naked. Lateral line complete, scales 40-49 ($\bar{x}$:44.3), all scales pored. Scales above lateral line to origin of first dorsal 4 or 5, to origin of second dorsal 5 to 7, usually 6, below lateral line to origin of anal 6 to 9, usually 7 or 8, and from 15 to 18, usually 17 or 18 around the caudal peduncle.

Pectoral fin always longer than head, rays 12 to 14, usually 13. Pelvic rays I, 5, spine and first two rays of breeding and non-breeding males and females with fleshy tips; that of spine especially prominent. First dorsal fin with 9 to 11, usually 10 spines, rather high and usually extending to base of second dorsal, the posterior membrane often attached to base of first ray of the second dorsal. Second dorsal large and higher than first dorsal, rays 11 to 14, usually 12. In adult males, the depressed second dorsal extends an appreciable distance posterior to the posterior margin of the anal fin, often reaching the base of the caudal fin. In females, the posterior margin of this fin is over or only slightly posterior to the anal. In both sexes, the origin of the second dorsal is slightly anterior to the anal origin. Anal smaller than second dorsal, rays II, 6 to 8, usually 7. First anal spine shorter and somewhat thicker than second, the second about half the length of the first ray. The caudal fin is almost always emarginate in adults, although it may grade from emarginate to truncate in sub-adults.

Cole (1957: 30) stated that the shape of the genital papilla was relatively constant throughout the subgenus <u>Boleosoma</u>. In <u>E</u>. <u>longimanum</u>, the anal opening in both sexes is surrounded by a round, radially grooved mound of tissue. In males, the genital papilla arises from the posterior base of this mound, and extends posteriorly to the fleshy base of the anal fin. It consists of a fleshy, flattened tube with a slight notch at its blunt tip indicating the genital opening. The papilla lies in a rather deep depression and is normally below the level of the body scales on either side. In females, the genital opening is located just posterior to the anal mound. Posterior to this opening, a fleshy, bilobed structure extends posteriorly almost to the anal origin. This papilla also lies in a deep depression, and surrounds the genital opening laterally and posteriorly. In breeding males, both the mound of tissue surrounding the anal opening and the genital papilla are swollen. Both these structures, while normally nonpigmented, become heavily pigmented at this time. In breeding females, the anal mound and genital papilla are also swollen, as is the tissue lying between the papilla and anal fin. The genital papilla of females was found to remain unpigmented throughout the year.

Raney and Lachner (1943: 235-236) reported that males and females of E. longimanum grew at about the same rate for the first year, with males averaging 37.6 mm and females 35.4 mm at the end of their first year. In the second year, males grew at a faster rate, averaging 54.9 mm to 46.3 mm for females. Few members of either sex were believed to live much beyond their second year.

Coloration

In females and non-breeding males, the spines of the first dorsal fin are clear. On each interradial membrane there is a vertical row of from 2 to 5 or 6 brownish orange spots. That portion of the membrane between and lateral to these spots is clear. In breeding males, the first three interradial membranes are dusky black from their base almost to their margin. The fourth, fifth, and sixth membranes are a slight dusky black, particularly along the margins of the spines. The spots mentioned above are now brick red and very noticeable on all but the first three membranes. The interradial membranes which are not dusky black are light tan in color.

The second dorsal fin in females and non-breeding males is similar in appearance to the first dorsal. The rays and interradial membranes are clear, with each membrane having a vertical row of from 4 to 8 brownish orange spots. In breeding males, the interradial membranes are tan and the spots are brick red. The entire fin has a thin black margin.

The pectoral fins of females and non-breeding males have clear interradial membranes. Melanophores are concentrated in groups upon the rays, giving the entire fin a barred appearance. This barring is much more prominent on the proximal half of the fin. In males, as breeding season approaches, the presence of additional malanophores gives the entire fin a dusky black appearance. At the height of breeding color, the interradial membranes are dusky black and the rays are dark black.

The pelvic fin is clear in females and non-breeding males, or there is only a slight scattering of melanophores on the rays. In breeding males, the pelvics are quiet similar to the pectorals, being dark black. The fleshy knobs on the spine and tips of the first two rays are white at this time.

The anal fin is clear in females and non-breeding males. In breeding males, the interradial membranes are jet black and the rays only slightly less black.

In females and non-breeding males, the interradial membranes of the caudal fin are clear. Small dark spots or elongate blotches are present on the rays and give the fin a light barred appearance. In breeding males, the caudal rays are dusky black and the interradial membranes are a yellowish orange.

Six black dorsal saddles cross the dorsal midline of the body and extend ventrally two or three scale rows on either side. The first saddle is located on the unscaled area just in front of the first dorsal; the second is slightly anterior to the middle of the first dorsal; the third is at the posterior fifth or sixth of the first dorsal and extends to or slightly posterior to the origin of the second dorsal; the fourth is anterior to the middle of the second dorsal. In females and sub-adult males, the fifth saddle lies under the posterior margin of the second dorsal fin. In adult males, the depressed second dorsal extends an appreciable distance posterior to this saddle. The sixth saddle lies on the caudal peduncle near the base of the caudal fin. From 8 to 12 (usually 8 or 9) separate black blotches extend along the lateral line from just posterior to the pectoral base to the posterior edge of the hypural. These blotches usually extend one scale row above and below the lateral line.

The dorsal background is golden tan, and grades to a light tan two or three scale rows below the lateral line. Ventral to these scale rows, the belly and breast are creamy white. Many of the scales above the lateral line are dark edged and often overlie dark brown to black blotches almost as large as the scales themselves. These dark scales and blotches are arranged in uneven broken lines. The first two or three scale rows below the lateral line are often dark edged and arranged in X and Y patterns. A dark, median basi-caudal spot is present, and is usually fused or only slightly separate from the posterior lateral blotch.

The top of the head from nape to tip of snout is a blotched golden brown. A preorbital black stripe runs from the eye onto the upper lip, where it is usually narrowly separate from the similar stripe on the other side of the head. The cheeks are flecked with golden brown and possess a suborbital golden brown spot. The opercle is rather heavily covered with melanophores which are concentrated to give a solid black appearance directly behind the preopercle. The lower jaw, chin, and branchiostegals are creamy white. A golden brown blotch lies on the fleshy area directly anterior to the pectoral fin base. This blotch often extends to or slightly underneath the posterior margin of the subopercle. A golden brown spot or vertical blotch is usually present on the anterior dorsal base of the pectoral fin.

In breeding males, the nape, cheeks, opercles, lower jaw, branchiostegal membranes, breast, and anterior scaleless half of the belly are a dark dusky black. The snout, interorbital region, and occiput are also dusky black, but are splotched with greenish tan. All scales from the head to caudal fin have a greenish blue margin. This margin is better developed and wider above the lateral line, becoming thinner and less noticeable toward the belly. The lateral blotches and dorsal saddles are less distinct and seem to grade into the general background color which ranges from tan to tannish orange.

Breeding Season

The breeding season of E. longimanum seems to fall sometime between the last of May and the first two weeks of June, although it is known that this can vary from year to year depending on water temperature. Examination of two females collected on June 1, 1952 from Looney Mill Creek, Botetourt County, Virginia, showed eggs to be well developed within the ovary. Females collected by the writer on May 29 and 30, 1964 from Johns Creek, Craig County, Virginia, had well developed eggs and swollen genital papillae, but little distention of the belly. On June 10, 1964 a large collection of E. longimanum was taken from Catawba Creek, Montgomery County, Virginia. Almost all adult females were distended to almost twice their normal width and their genital papillae were very swollen. Several males were in full breeding color, and several others were approaching full breeding color. It is believed that this collection was taken very close to actual spawning time. Several collections were examined which were taken on July 19 and July 20, 1963 from Jackson River, Highland County, Virginia. All adults in these collections had completed spawning.

Specimens Examined

Back Creek

176 - Back Creek on route 600, 8 miles north of route 84 intersection, Highland Co., Virginia, August 16, 1962, J. E. Carico, Glenn Clemmer, Ed McConnell, 7 specimens.

Big Back Creek

175 - Big Back Creek along state 600, 2 air miles north of Mountain Grove, Bath Co., Virginia, August 16, 1962, J. E. Carico, Ed McConnell, Glenn Clemmer, 1 specimen.

Catawba Creek

1604 - Catawba Creek at route 311 crossing 1/2 road mile from junction 311 and 277 east of Catawba, Roanoke Co., June 10, 1964, R. L. Miles, C. Heartwell, T. J. Clayton, 20 specimens.

Craig Creek

192 - Craig Creek at Pinetop, 2 air miles northeast Newcastle, Craig Co., Virginia, May 11, 1963, R. E. Jenkins, F. W. Inge, 1 specimen.

193 - Craig Creek 1.3 air miles northeast of Newcastle, 1.9 air miles southwest Va. Mineral Springs, Craig Co., Virginia, May 15, 1963, R. E. Jenkins, F. W. Inge, 2 specimens.

194 - Craig Creek 0.25 river miles downstream from Pinetop, enter dirt road paralleling river by way of Whitelow's driveway, Craig Co., Virginia, June 6, 1963, R. E. Jenkins, J. E. Carico, R. L. Miles, 2 specimens.

1006 - Craig Creek at steel bridge 6.8 miles ________ Newcastle on route 311, Craig Co., Virginia, August 19, 1958, R. D. Ross, J. Wakeman, K. Cook, 2 specimens.

1423 - Craig Creek 1.3 air miles northeast of Newcastle, 1.9 air miles southwest of Virginia Mineral Springs, Craig Co., Virginia, October 12, 1960, V.N.H. class, 4 specimens.

Jackson River

196 - Jackson River 0.5 mi. north of Highland-Bath Co. line at steel bridge on route to Bolar, Highland Co., Virginia, July 19, 1963, R. E. Jenkins, R. D. Ross, 10 specimens.

198 - Jackson River 7 road miles south of Monterey on route 220, Highland Co., Virginia, July 19, 1963, R. E. Jenkins, R. D. Ross, 2 specimens.

1575 - Jackson River at Hidden Valley Farm, 4.3 miles north of Mitcheltown, Bath Co., Virginia, July 20, 1963, R. E. Jenkins, R. D. Ross, 1 specimen.

197 - Jackson River along route 220, 1.5 road miles south Pinckney, Highland Co., Virginia, July 19, 1963, R. E. Jenkins, R. D. Ross, 11 specimens.

Johns Creek

1666 - Johns Creek 2 road miles northeast of Newcastle, second bridge crossing upstream from Newcastle, Craig Co., Virginia, May 30, 1964, R. E. Jenkins, R. L. Miles, C. Heartwell, 2 specimens.

1668 - Johns Creek 1 road mile northeast of Maggie on county road 632, 1 mile northeast junction of county roads 632 and 656, Craig Co., Virginia, May 29, 1964, R. L. Miles, R. E. Jenkins, 5 specimens.

Looney Mill Creek

WSD15 - Looney Mill Creek 5 1/2 miles southeast Fincastle, Botetourt Co., June 1, 1952, B. Stough, W. S. Davis, 2 specimens.

Potts Creek

877 - Potts Creek 1 mile below Paint Bank on Mr. Smith's property, Craig Co., Virginia, August 21, 1957, R. D. Ross, K. Cook, J. Wakeman, 1 specimen.

1009 - Potts Creek 2.8 road miles northeast of Paintbank, Craig Co., Virginia, August 19, 1958, R. D. Ross, J. Wakeman, K. Cook, 1 specimen.

Rockfish River

JPT1 - Rockfish River 20 miles southwest of Charlottesville, Nelson Co., Virginia, October 20, 1951, J. P. Thompson, 20 specimens.

Woods Creek

1011 - Woods Creek at Lexington, trib. of Gauley (North) River, Rockbridge Co., Virginia, August 21, 1958, 5 specimens.

ETHEOSTOMA PODOSTEMONE

Synonymy

Etheostoma podostemone - Jordan, 1889: 359-360 (original description; subgenus Boleosoma; "allied to E. longimane"; locality records). Jordan, 1890: 98 (referred to original description; locality records); 121 (abundant in Bottom Creek); 124 (range; habitat notes); Plate XV, fig. II. Fowler, 1923: 10-11 (disagrees with Jordan and Evermann on distinguishing features between E. longimanum, E. podostemone, and E. nigrum). Bailey and Gosline, 1955: 15 (subgenus Boleosoma; vertebral counts); 38-39 (locality records). Cole, 1957: 217-218: (synonymy); 219 (type material; range; diagnosis); 219-221 (material examined). Moore, 1957: 184 (key to identification); 189 (brief description; range). Eddy, 1957: 209 (brief description; range). Gilbert, 1961: 456 (companion form of E. longimanum; possible evolutionary history).

Boleosoma podostemone - Jordan and Evermann, 1896a: 361 (range; reference to original description). Jordan and Evermann, 1896b: 1005 (description; synonymy; range; habitat notes). Cockerell, 1914: 155 (locality records). Cockerell and Elder, 1914: 157 (range; comparison of scales). Jordan, 1916: 356 (range). McGauhey et al., 1942: 96 (locality records). Raney and Lachner, 1946b: 220 (endemic of Roanoke River). Raney, 1950: 177 (probably limited to Roanoke River); 187 (in list of fishes found only in Roanoke River).

Ulocentra podostemone - Jordan, 1929: 158 (description; range; abundant in Podostemon).

Ulocentra podostemona - Pratt, 1935: 121 (description; range).

Cottogaster podostemone - Fowler, 1945: 37 (range; James River in error).

Types

In his original description, Jordan (1889: 359) designated as types USNM 39863. Cole (1957: 219) reported that this collection was still extant in the U. S. National Museum under the original number and consisted of 5 specimens, all valid podostemone. He designated as lectotype "a sub-adult male, 39.5 mm in st. length with lateral line count of 39, anal fin count, 2 spines, 6 soft rays, first dorsal 9 and second dorsal soft rays 12." Due to the recent reexamination of these specimens, and to the fact that Cole reported them to be brittle and badly shrunken, the types were not examined by the writer during the course of this study.

Range

Etheostoma podostemone is endemic to the Roanoke River system in Virginia and North Carolina. Figure 36, p.128 shows most of the available collection records from both the literature and the V. P. I. collection records and gives some idea of the known distribution of E. podostemone within the Roanoke River system. Like E. longimanum, it is widely distributed in the upstream portion of its respective stream system and is limited to those streams or stream segments which flow through the Blue Ridge Mountains and outlying mountainous regions of the Piedmont.

Habitat

Jordan (1889b: 359; 1890: 126) reported that E. podostemone inhabitated swift water, especially among rocks covered by river weed. From collections taken by the writer, it appears that E. podostemone prefers the smaller tributary streams of the Roanoke. It is usually found in habitats almost identical with those of E. longimanum; inhabiting the deeper riffles of from 6 inches to 2 feet in depth with a moderate to moderately fast current, and being especially abundant in riffles containing flat rocks with openings underneath them.

Description

The body of E. podostemone is moderately elongate and little compressed, with greatest body depth 15.6-20.1% ($\bar{x}$:18.2%) of standard length and caudal peduncle depth 9.4-11.9 ($\bar{x}$: 11.1%) of standard length. The largest male examined was 62.8 mm and the largest female 55.0 mm in standard length. Head length is moderate, $\bar{x}$: 24.6% in standard length. The snout is blunt and rather wide, profile rounded; length almost always less than diameter of orbit. The premaxillaries are protractile and the maxillaries usually reach to the front of the eye. The mouth is small, horizontal, and slightly subterminal, with teeth being present on the premaxillae, vomer, palatines, and dentary. The gill membranes are rather broadly connected and there are 6 branchiostegal rays. The preopercle is entire.

The lateral line system of the head is very similar to that of E. longimanum. The lateral canal is complete and opens in five pores. The supratemporal is complete and opens in a median and two lateral pores. The anterior nasal pore of the supraorbital canal opens before and on line with the anterior nostril; the posterior nasal pore opens anterior to and above the posterior nostril; the interorbital lies just anterior to the middle of the eye, and the postorbital pore opens just posterior to the orbit. The coronal pore was present in all specimens examined, and while often opening anterior to the posterior margin of the eye, it frequently opened as far posteriorly as the posterior margin of the orbit, lying on a line with the postorbital pores. This condition was never seen in _E. longimanum_. The infraorbital canal is complete and opens in 8 pores, almost identical in location to those of _E. longinamum_. The preoperculomandibular canal is also complete and is similar in location to that of _E. longimanum_. It opens in from 7 to 11, usually 9 pores, with a pore at its origin above the preopercle, 5 pores opening along the edge of the preopercle, and usually only 3 pores opening on the lower jaw.

The cheeks, nape, breast, and anterior half of the belly are naked, while the opercles are scaled. The lateral ine is complete, with 35-41 ($\bar{x}$: 38.6) scales, all of which are pored. Scales above lateral line to origin of first dorsal 3 to 5, usually 4, to origin of second dorsal 4 to 6, usually 5, below lateral line to origin of anal 5 to 8, usually 6 or 7, and from 14 to 18, usually 16 scale rows around the narrowest part of the caudal peduncle.

Pectoral fin always longer than head, rays 10 to 13, usually 12. Pelvic rays I, 5, spine and first two rays of breeding and non-breeding males and females with fleshy tips. First dorsal moderately high, with 8 to 11, usually 9 or 10 spines, extending to or almost to origin of second dorsal. Second dorsal larger and higher than first dorsal, rays

10 to 14, usually 12 or 13. As in E. longimanum, the depressed second dorsal fin of adult males extends posterior to the posterior margin of the anal fin, almost reaching the caudal base. In females and sub-adult males, this fin extends only slightly posterior to the anal margin. In both sexes, the origin of the second dorsal fin is slightly anterior to the anal fin origin. Anal fin smaller than soft dorsal, rays II, 5 to 8, usually 6 or 7. First anal spine shorter and somewhat thicker than second, the second about 1/2 the length of the first anal ray. The caudal fin ranges from truncate to rounded in sub-adults, while in adults the posterior margin is almost always rounded.

The description of the genital papilla of E. longimanum (p. 25), serves also for E. podostemone. No significant differences could be distinguished between the papillae of the two species.

Coloration

In females and non-breeding males, the spines of the first dorsal fin are essentially clear. The interradial membranes are clear and each membrane possesses a vertical row of brownish orange spots or small blotches. These spots vary greatly in number from individual to individual; the longest interradial membrane of one specimen may have only a basal and median spot, while the same membrane of another specimen possesses 5 or 6 spots. No correlation was seen between the number and arrangement of these spots and the sex or size of the individual. The entire first dorsal fin has a wide brownish orange margin. In breeding males, the first three interradial membranes are quiet black almost to their margins. The remaining interradial membranes are tannish orange and possess a dusky basal band. The vertical rows of spots and the marginal band are brick red.

The second dorsal fin in females and non-breeding males is similar to the first dorsal in many respects. The rays have melanophores grouped in small vertical blotches, giving them a slightly barred appearance. The interradial membranes are clear and each membrane has a vertical row of from 2 to 8 brownish orange spots. In breeding males, the interradial membranes are light orange, and the spots are brick red. The entire fin has a thin black margin which was not present in females or non-breeding males.

In females and non-breeding males, the interradial membranes of the pectoral fin are clear. Melanophores are concentrated on the rays, giving the fin a barred appearance. These bars are darker and more prominent on the proximal half of the fin. In breeding males, the interradial membranes seem to remain clear. The rays are slightly dusky, but the elongate black bars are still easily distinguishable. It may well be that the males examined were not in full breeding color, and the pectorals would have been much darker later in the year, as are the pectorals of _E_. _longimanum_ and the pelvics and anal of _E_. _podostemone_.

The pelvic fins of females and non-breeding males are clear or only slightly marked by melanophores scattered on the rays. In breeding males, the rays are dusky black and the membranes jet black. The fleshy knobs on the spine and tips of the first two rays are white.

Both the membranes and rays of the anal fin are clear in females and non-breeding males. In breeding males, the entire fin is dark to dusky black.

The caudal fin of females and non-breeding males has a series of elongate, separate brownish orange spots on the rays which extend laterally onto the interradial membranes, giving the fin a barred appearance. In breeding males, the interradial membranes, which were clear in females and non-breeding males, are light orange. The spots on the rays and membranes are brick red, and the entire fin has a thin black margin.

The body coloration of females and non-breeding males is quiet similar. The dorsal background of yellowish tan extends two or three scale rows below the lateral line. Ventrally, the belly and breast are creamy white. Six black dorsal saddles cross the back and extend ventrally two or three scale rows on either side. Each of these saddles is located at approximately the same position as those of E. longimanum (p. 27). From 6 to 11, usually 8 or 9 separate black blotches extend along the lateral line from the pectoral base to the posterior edge of the hypural. These blotches are from two to four scale rows in width and extend approximately one scale row on either side of the lateral line. Both the dorsal saddles and lateral blotches are less compact and distinct in E. podostemone than in E. longimanum. Many scales above the lateral line and from two to three scale rows below the lateral line posterior to the anal fin origin are dark edged and overlie dark brown to black blotches almost as large as a single scale. In females and non-breeding males, these blotches are arranged in irregular, broken rows above the lateral line, and appear as scattered spots below. A dark, median basi-caudal spot is present.

The top of the head and snout are blotched with golden tan and dark brown in males and non-breeding females. A preorbital black stripe runs from the eye onto upper lip, where it may or may not fuse with the stripe from the other side. A dark brown suborbital bar extends from the orbit to the ventral surface of the cheek, and a small golden brown spot is usually located just posterior to the eye. The scaled area of the opercle is black, the ventral margin creamy white, and the posterior margin golden brown. The branchiostegals, lower jaw, and chin are creamy white. A golden brown bar is located before and behind the pectorals. In adults, the prepectoral bar often extends ventrally to the lateral margin of the breast, while in younger individuals it often consists of two golden brown spots between the pectoral fin and opercle; these two spots fusing and elongating with age. The postpectoral bar varies greatly from individual to individual. In some cases it may merely consist of a small brown spot posterior to the ventral margin of the pectoral, while in others it consists of a brown bar running the full width of the pectoral fin. There seems to be little correlation between either sex or size and the development of this bar.

In breeding males, the nape is dusky brown and the breast, cheeks, head, and scaleless half of the belly are dusky black. The dark, round spots or blotches underlying separate scales are now more distinct and occur under each scale above the lateral line. Below the lateral line, they occur posterior to the anal fin origin and completely encircle the caudal peduncle. These blotches are arranged in parallel rows, and their appearance was adequately described by Cole (1957: 215) "as regularly distributed dots placed in a checkerboard pattern." This pattern, as well as the black blotches on the first three interradial membranes of the first dorsal fin was distinguishable in several fresh specimens collected as late as August 11. Preserved specimens which had been collected as late as October 14 and as early as April 6 had both characters well developed. Although it seems that these two characters are characteristic of breeding coloration, both may be retained by adult males throughout most of the year.

Breeding Season

The breeding season of E. podostemone seems to occur during the last two weeks of May and possibly the first week of June. A collection taken May 23, 1964 from the South Fork of Roanoke River, Montgomery Co., Virginia, contained several males in full breeding color and many females with swollen genital papillae and greatly distended bodies. A later collection taken June 12, 1964 from Storys Creek, Franklin Co., Virginia, had completed spawning, although the female genital papillae were swollen and the males retained some breeding color.

Specimens Examined

Back Creek

1464 - Back Creek at 657 crossing 0.5 mile from 220 intersection near Red Hill Church, 4.3 air miles NNE of Boone's Mill, Roanoke County, Virginia, July 3 1961, Glen Clemmer, Paul Fletcher, and R. D. Ross, 3 specimens.

Big Otter Creek

992 - Big Otter Creek at Route 43 crossing 4.3 road miles NNW of junction of 460 and 43 in Bedford at junction of 43 and county road 682. Bedford Co., Virginia, June 25, 1964, R. D. Ross, J. Wakeman, and Harry Sowers, 2 specimens.

1692 - Big Otter Creek on Route 460 crossing 6.9 road miles east of center of town of Bedford, Bedford Co., Virginia, June 25, 1964, Robert Miles, Paul Buhan, Ed.McConnell, and R. D. Ross, 5 specimens.

Blackwater River

1465 - Blackwater River at Blaine, 3.2 air miles NE by N of Rocky Mount, low water bridge at rocket fuel plant, Franklin Co., Virginia, July 4, 1961, Glenn Clemmer, Paul Fletcher, and R. D. Ross, 8 specimens.

1466 - Gills Creek 3.2 river miles above mouth in Blackwater River, 5 air miles SE Hales Fort Church, 1.9 air miles SW of Schruggs, Franklin Co., Virginia, July 6, 1961, Glenn Clemmer, Paul Fletcher, and R. D. Ross, 4 specimens.

1475 - Blackwater River on county road 655 crossing near Crafts Church, 7.8 air miles W of Bedford-Franklin-Pittsylvania Co. line, Franklin Co., Virginia, July 6, 1961, Glenn Clemmer, Paul Fletcher, and R. D. Ross, 5 specimens.

1477 - Blackwater River at gaging station 5.0 air miles W of Franklin-Bedford-Pittsylvania Co. line, 2.8 air miles SW by S of Schruggs, Franklin Co., Virginia, July 5, 1961, Glenn Clemmer, Paul Fletcher, and R. D. Ross, 1 specimen.

1478 - Blackwater River low water bridge, 616 crossing 1.2 air miles SW by W of Franklin-Bedord-Pittsylvania Co. line, 3.8 air miles SE Schruggs, Franklin Co., Virginia, Glenn Clemmer, Paul Fletcher, and R. D. Ross, 1 specimen.

950 - Blackwater River at 670 crossing 2.7 river miles above mouth of Gills Creek and 2.7 air miles N. Union Hall, 7.2 miles S. Haleford, 10.1 air miles SSW Moneta, Franklin Co., Virginia, July 11, 1958, R. D. Ross, J. Wakeman, and K. Cook, 1 specimen.

1751 - Blackwater River at intersection of 737, 643 and 732, Franklin Co., Virginia, October 15, 1961, Glenn Clemmer, Bob Jenkins, Jim Roth, and Charlie Heartwell, 1 specimen.

1753 - Blackwater River 1 air mile east of Calloway on 740, Franklin Co., Virginia, October 15, 1961, Glenn Clemmer, Bob Jenkins, Jim Roth, and Charlie Heartwell, 1 specimen.

1754 - Blackwater River at 740 crossing 1.8 air miles east of Calloway, Franklin Co., Virginia, October 15, 1961, Glenn Clemmer, Bob Jenkins, Jim Roth, and Charlie Heartwell, 2 specimens.

190 - Blackwater River at Rocketfuel Plant, Papko Roanoke Labs, Franklin Co., Virginia, April 6, 1963, V.N.H. Class, 9 specimens.

1562 - North Fork Blackwater River at 850 crossing, 1 air mile NNW of Dillons Mill, Franklin Co., Virginia, September 8, 1961, Glenn Clemmer, Paul Fletcher, and Tom Perkins, 2 specimens.

1752 - North Fork of Blackwater River 3 air miles NNE of Calloway, Franklin Co., Virginia, October 14, 1961, Glenn Clemmer and Bob Jenkins, 5 specimens.

1755 - North Fork of Blackwater River on 641, 2 air miles NE of Calloway, Franklin Co., Virginia, October 14, 1961, Glenn Clemmer and Bob Jenkins, 6 specimens.

<u>Pigg River</u>

1672 - Storys Creek, tributary of Pigg River, 1.3 air miles south of Rocky Mount on county road 619, Franklin Co., Virginia, June 12, 1964, R. L. Miles, Ed McConnell, and R. D. Ross, 10 specimens.

<u>North Fork Roanoke River</u>

528 - North Fork Roanoke River 7 miles SE Blacksburg, 0.7 miles SW Ironto, Montgomery Co., Virginia, October 17, 1953, V.N.H. Class, 3 specimens.

389 - North Fork Roanoke River at McDonald's Mill, Montgomery Co., Virginia, October 10, 1951, 2 specimens.

<u>Roanoke River</u>

195 - Roanoke River at county road 639 crossing, 1 air mile west Bend Union Church, 1 air mile northeast Holiness

Church, Roanoke Co., Virginia, June 28, 1963, D. Dudak, F. S. Settle, and R. E. Jenkins, 7 specimens.

South Fork Roanoke River

1414 - South Fork Roanoke River about 100 yards below county road 609 crossing south of Shawsville, Montgomery Co., Virginia, October 5, 1960, V.N.H. Class, 5 specimens.

393 - South Fork Roanoke River 7 3/4 miles east of Christiansburg, 2 miles south of Shawsville, 3/4 mile north of Alleghany Springs, Montgomery Co., Virginia, October 16, 1951, N. Swink, W. Davis, and R. D. Ross, 5 specimens.

1003 - South Fork of Roanoke River above mouth of Bony's Run, 0.7 miles SE Shawsville, Montgomery Co., Virginia, August 12, 1958, R. D. Ross, J. Wakeman, and K. Cook, 3 specimens.

1004 - South Fork Roanoke River 1 mile south Elliston near BM 1282, Montgomery Co., Virginia, August 12, 1958, R. D. Ross, J. Wakeman, and K. Cook, 5 specimens.

1560 - South Fork Roanoke River 2.0 miles NNE Shawsville, Montgomery Co., Virginia, October 10, 1961, V.N.H. Class, 3 specimens.

401 - South Fork Roanoke River from 1/4 mile above Allegheny Springs to 1/2 mile below, Montgomery Co., Virginia, October 27-28, 1955, Bill Keeton, Bill Lund, and R. D. Ross, 24 specimens.

COMPARATIVE DIAGNOSIS

Etheostoma longimanum and E. podostemone are separable from each other at Ginsburg's specific level in the following characters:

1. Lateral line scales (Table 1, Figs. 1 and 31a.) E. longimanum ranges from 40 to 49, usually 42 to 46, mean 44.3. E. podostemone ranges from 35 to 41, usually 37 to 41, mean 38.6. Average percentage of overlap 4.8.

2. Number of primary scale rows above the lateral line from D_1 origin to D_2 origin (Table 6, Figs. 6 and 31f). E. longimanum ranges from 14 to 18, usually 15 to 17, mean 16.4. E. podostemone ranges from 11 to 15, usually 12 to 14, mean 13.5. Average percentage of overlap 4.4.

3. Number of pelvic fin rays (Table 11 and 12, Figs. 11-12 and 32d and e). E. longimanum ranges from 12 to 14, usually 13, mean 13.2 for both right and left pelvic fins. E. podostemone ranges from 10 to 13, usually 12, mean 12.1 for both right and left pelvic fins. Average percentage of overlap: right pectoral rays 5.8, left pectoral rays 8.0.

E. longimanum and E. podostemone are separable from each other in the following characters whose overlap is intermediate between the specific and subspecific level of Ginsburg's criteria.

1. Scale rows above lateral line to origin of second dorsal fin (Table 3, Figs. 2 and 31c). E. longimanum ranges from 5 to 7, usually 6, mean 5.9. E. podostemone ranges from 4 to 6, usually 5, mean 5.1. Average percentage of overlap 10.4.

2. Caudal peduncle scales, plus scales above lateral line to origin of D_2 plus scales below lateral line to origin of anal fin (Table 7, Figs. 7

and 31g). *E. longimanum* ranges from 27 to 33, usually 29-32, mean 30.6. *E. podostemone* ranges from 24 to 31, usually 26-29, mean 27.6. Average percentage of overlap 11.9.

3. Number of preoperculomandibular pores (Table 14, Figs. 14 and 32g). *E. longimanum* ranges from 9 to 10, almost always 10, mean 9.9. *E. podostemone* ranges from 8 to 11, usually 9, mean 9.1. Average percentage of overlap 13.1.

4. Lower jaw length in head length (Table 29, Figs. 29 and 34f). *E. longimanum* ranges from 21.3 to 26.7%, mean 24.7%. *E. podostemone* ranges from 19.2-24.6%, usually 21.3 to 23.7%, mean 22.4%. Average percentage of overlap 13.0.

E. longimanum and *E. podostemone* are differentiated at Ginsburg's subspecific level in the following characters:

1. Rays in anal fin (Table 10, Figs. 10 and 32c). *E. longimanum* ranges from 6 to 8, usually 7 or 8, mean 7.2. *E. podostemone* ranges from 5 to 8, usually 6 or 7, mean 6.4. Average percentage of overlap 19.8.

2. Scale rows around caudal peduncle (Table 5, Figs. 5 and 31e). *E. longimanum* ranges from 15 to 19, usually 16 to 18, mean 17.1. *E. podostemone* ranges from 14 to 18, usually 15 to 17, mean 16.0. Average percentage of overlap 15.8.

3. Predorsal length in standard length (Table 26, Figs. 26 and 34g). *E. longimanum* ranges from 30.1 to 34.3%, mean 32.4%. *E. podostemone* ranges from 28.7 to 33.5%, mean 30.8%. Average percentage of overlap 20.3.

4. Caudal peduncle depth in standard length (Table 16, Figs. 16 and 33b). E. longimanum ranges from 8.8 to 11.2%, mean 10.3%. E. podostemone ranges from 9.4 to 11.9%, mean 11.1%. Average percentage of overlap 22.1.

5. Snout length in standard length (Table 19, Figs. 19 and 33e). E. longimanum ranges from 5.3 to 7.4%, mean 6.3%. E. podostemone ranges from 4.7 to 6.4%, mean 5.4%. Average percentage of overlap 22.1.

6. Snout length in head length (Table 27, Figs. 27 and 34d). E. longimanum ranges from 21.5 to 26.6%, mean 24.1%. E. podostemone ranges from 19.4 to 23.9%, mean 22.2%. Average percentage of overlap 20.0.

7. Length of longest pelvic fin ray in standard length (Table 22, Figs. 22 and 33h). E. longimanum ranges from 19.9 to 27.4%, usually 22.4 to 24.9%, mean 23.9%. E podostemone ranges from 18.9 to 27.4%, usually 19.9 to 23.4%, mean 21.8%. Average percentage of overlap 22.7.

The following characters show an overlap which is intermediate between Ginsburg's subspecific and racial levels:

1. Spines in first dorsal fin (Table 8, Figs. 8 and 32a). E. longimanum ranges from 9 to 11, usually 9 or 10, mean 9.8. E. podostemone ranges from 8 to 11, usually 9 or 10, mean 9.2. Average percentage of overlap 29.8.

2. Scale rows below lateral line to origin of anal fin (Table 4, Figs. 4 and 31d). E. longimanum ranges from 6 to 9, usually 7 or 8, mean 7.5. E. podostemone ranges from 5 to 8, usually 6 or 7, mean 6.6 Average percentage of overlap 28.7.

E. longimanum and E. podostemone are differentiated at Ginsburg's racial level in the following two characters:

1. Head length in standard length (Table 18, Figs. 18 and 33d). E. longimanum ranges from 23.4 to 28.2%, mean 25.4%. E. podostemone ranges from 22.8 to 27.3%, mean 24.6%. Average percentage of overlap 32.7.

2. Longest pectoral fin ray length in standard length (Table 21, Figs. 21 and 33g). E. longimanum ranges from 25.7 to 39.0%, mean 32.9%. E. podostemone ranges from 25.0 to 34.8%, mean 30.8%. Average percentage of overlap 35.0.

The following characters show complete or almost complete overlap and are of no significant value in separation of the two species:

1. Rays in second dorsal fin (Table 9, Figs. 9 and 32b). E. longimanum ranges from 11 to 14, usually 11 or 12, mean 11.9. E. podostemone ranges from 10 to 14, usually 12 or 13, mean 12.4. Average percentage of overlap 86.4.

2. Number of infraorbital pores (Table 13, Figs. 13 and 32f). E. longimanum ranges from 7 to 9, usually 8, mean 8.0. E. podostemone ranges from 7 to 9, usually 8, mean 8.0. Average percentage of overlap 100.

3. Postorbital head length in standard length (Table 20, Figs. 20 and 33f). E. longimanum ranges from 12.4 to 15.1%, mean 13.6%. E. podostemone ranges from 12.4 to 15.4%, mean 13.6%. Average percentage of overlap 94.9.

4. Length of orbit in head length (Table 28, Figs. 28 and 34e). E. longimanum ranges from 23.8 to 28.6% mean 25.9%. E. podostemone ranges from 22.3 to 28.3%, mean 25.0%. Average percentage of overlap 100.

5. Head depth in standard length (Table 17, Figs. 17 and 33c). E. longimanum ranges from 14.5 to 18.4%, mean 16.3%. E. podostemone ranges from 14.8 to 16.9%, mean 15.8%. Average percentage of overlap 100.

6. Caudal peduncle length in standard length (Table 25, Figs. 25 and 34c). E. longimanum ranges from 25.2 to 29.7%, mean 27.4%. E. podostemone ranges from 24.6 to 29.7%, mean 27.3%. Average percentage of overlap 100.

7. Body depth in standard length (Table 15, Figs. 15 and 33a). E. longimanum ranges from 16.8 to 20.7%, mean 18.6%. E. podostemone ranges from 15.6 to 20.1%, mean 18.2%. Average percentage of overlap 89.2.

8. Length of first dorsal fin base in standard length (Table 23, Figs. 23 and 34a). E. longimanum ranges from 24.7 to 30.7%, mean 27.7%. E. podostemone ranges from 24.4 to 30.4%, mean 27.2%. Average percentage of overlap 98.5.

In the process of measuring the length of the depressed second dorsal fin of males, it was noticed that this fin varied greatly in length with respect to the standard length of the individual. By plotting the length of this fin in standard length against the standard length (Fig. 30), it was shown that in both species the percent of standard length increased with increased standard length. If this graph is divided horizontally at 53.0 mm standard length, 87.2 percent of all males greater than 53.0 mm in standard length have a depressed second dorsal fin length of 36.0 percent or more of standard length. In individuals 53.0 mm or less in standard length, 90.0 percent of all males have a depressed second dorsal fin length of less than 36 percent of standard length. The mean for this character appears significantly different between the two groups, being

39.0 percent for males of both species greater than 53 mm in standard length and 32.8 percent for males less than 53 mm in standard length. This allometric growth was not reported by Cole (1957), and it is evident that proportional measurements of this character would be unreliable for comparative purposes unless allometric growth was taken into consideration. This character was not compared for the two species in this study.

E. longimanum is a finer scaled species than *E. podostemone*, and both species can be separated on the species or intermediate species level in seven characters. They also differ on the subspecific level in seven of the characters studied. While these subspecific differences do not indicate the differentiation that the specific differences do, they are useful in separating the two species and serve to indicate genetic differences between them. Of the nine characters found to lie on the racial and subracial levels of differentiation and which show little or no difference in either species, seven were morphometric characters. In geminate species, such as *E. longimanum* and *E. podostemone*, occupying such seemingly similar niches, we might expect less differentiation in morphometrics than in other characters. Hubbs and Cannon (1935) found morphometric characters to be of little value in separation of the nine species within the genera *Hololepis* and *Villora*, and Collette (1962) did not include proportional measurements in his reevaluation of *Hololepis*.

In addition to the quantitative differences, several qualitative characters serve to separate *E. longimanum* from *E. podostemone*. One of the most distinct differences is the presence of a suborbital bar in *E. podostemone* extending from the ventral margin of the orbit to or onto the ventral surface of the cheek. In *E. longimanum*, this bar is replaced by a less distinct round suborbital blotch which is located on the middle of the cheek, extending neither dorsally to the orbit or ventrally to the ventral surface of the cheek. This difference holds true for all specimens examined, and proved to be one of the easiest to use characters in identification of specimens. *E. podostemone* also possesses a postpectoral spot or bar which was never seen in *E. longimanum*. The presence in males, especially during the breeding season, of a checkerboard pattern of round blotches above the lateral line and below the lateral line posterior to the anal fin origin, is another distinct character of *E. podostemone*. This coloration pattern was never seen in *E. longimanum*, and Cole (1957: 215) stated that it was not present in any other member of the subgenus *Boleosoma* which he studied. The lateral blotches and dorsal saddles seem more distinct in *E. longimanum*, while the spots on the membranes on the first and second dorsal, pectorals, and caudal fins are darker and more distinct in *E. podostemone*, giving the caudal and pectoral fins a more noticeable barred appearance. The snout of *E. podostemone* is somewhat shorter than that of *E. longimanum*, and the profile forms a gently rounded slope. In *E. longimanum*, the profile is steep and more nearly vertical. This character does not hold true for all specimens, especially in individuals less than 35 mm in standard length. Finally, the shape of the caudal fin seems to set the two apart. In *E. longimanum*, the caudal fin is almost alway emarginate, especially in adults. In *E. podostemone*, the caudal fin ranges from truncate to rounded in sub-adults, but in most cases, particularly in large adults, the caudal fin margin is distinctly rounded.

CONCLUSIONS AND RELATIONSHIPS

E. longimanum and E. podostemone are considered by the writer to represent valid species. The many morphological similarities between the two, as well as their restriction to adjacent drainage systems, seems to indicate a common ancestral stock. Cole (1957: 213; 228) reported that E. longimanum and E. podostemone, while distinctly separated from the E. nigrum and E. olmstedi complexes of the eastern United States, seemed to be most closely related to E. olmstedi. He based this primarily on the complete infraorbital canals of these three species. He also stated that E. longimanum and E. podostemone probably diverged from early olmstedi-like forms which were adapted to a mountain habitat. This separation was enhanced by the introduction of E. nigrum into both the James and Roanoke Rivers from the New River system by stream captures. Gilbert (1961: 456) also postulated a common ancestral stock for the two species. He suggested that this stock probably reached the Roanoke and James from the preglacial Teays system, whose upper part occupied virtually the same channel as that of the present day New River.

The fact that E. podostemone and E. longimanum seem to be more closely related to E. olmstedi than to E. nigrum, plus the present distribution of boleosomines in the eastern United States seems to favor Cole's theory of origin. E. nigrum is a widely distributed species west of the Appalachian Mountains in the Mississippi and Ohio River systems and the Great Lakes region. East of the Appalachian Mountains it is represented by headwater forms in the James, Roanoke, Tar, Neuse, Yadkin, and Catawba Rivers. Cole (1957) designated as subspecies E. nigrum roanokense in the

Roanoke and E. nigrum jamesense in the James. These two forms occur sympatrically with E. podostemone and E. longimanum respectively, and the range of both species overlaps almost completely in the two separate river systems. Cole's (1957) theory that E. nigrum was introduced into the James and Roanoke Rivers from New River by stream piracies seems to best explain the presence of this western form in the upland portions of these Atlantic coast streams. Wright (1931: 207-208; 1934: 50-69; 1936: 98) reported that an area of approximately 200 square miles of New River drainage has been abstracted by the Roanoke River through stream piracy. This included piracies by both the North and South Forks of the Roanoke River. He also reported possible piracies of New River tributaries in high-lying valleys by headwater streams of the James River system. However, E. nigrum is presently limited in its distribution within New River. Ross and Perkins (1957) did not record any Boleosoma in over 150 collections taken from the New River system of Virginia. They found the fauna of this area to be quiet depauperate and gave loss of water to subsurface drainages and high concentration of dissolved sulfates as possible causes of this reduction. Addair (1944) reported only two collections of E. nigrum from the New River system of West Virginia above Kanawha Falls, although he found it to be a common species below the falls. He also noted the rather depauperate fauna of this river system and gave high water velocity, steep gradient, scarcity of aquatic plant life, narrow flood plains, and pollution as possible limiting factors. Transfer of E. nigrum to the Roanoke and James Rivers must have occured at a time when ecological conditions were less severe and E. nigrum was widely distributed in upper reaches of New River.

Cole (1957) also raised *E. olmstedi*, formerly considered a subspecies of *E. nigrum*, to full species rank. He found *E. olmstedi* to be represented by two subspecies in the Roanoke and James Rivers. *E. olmstedi olmstedi* inhabits smaller tributary streams of the Piedmont and Coastal Plain in both systems, and *E. olmstedi atromaculatum* is widely distributed in both rivers below the fall line. Both subspecies have a wide distribution in the eastern United States, with *olmstedi olmstedi* ranging from the Merrimack River of Massachusetts to the New River drainage in North Carolina, and *olmstedi atromaculatum* ranging from the lower Hudson to the lower Roanoke River. Cole reported intergradation occuring sporadically between these two subspecies in most of the river systems which they occupy. He also noted that although *E. o. olmstedi* is an inhabitant of upland streams from the Potomac River north, it is limited to downstream areas in rivers south of the Potomac. He suggested that the introduction of *E. nigrum* forms into these streams might have restricted its range.

While *E. o. olmstedi* is presently limited to the downstream regions of the Roanoke and James Rivers and apparently does not overlap the range of *E. longimanum* and *E. podostemone*, it seems possible that this form may have at one time been an inhabitant of the montane regions of both rivers as it is in the streams of the northern part of its range. This species could have begun to differentiate into an upstream and a downstream stock in both river systems. A later introduction of *E. nigrum* from the New River could have further enhanced separation and led to speciation of *E. longimanum* in the James and *E. podostemone* in the Roanoke. The original stock, presently recognized as *E. o. olmstedi* was restricted to the lower reaches of both river systems.

This theory of origin necessitates speciation of the two forms studied from *olmstedi* stock. The tendency of *E. olmstedi* to differentiate under different ecological conditions is shown by the fact that *E. olmstedi olmstedi* and *E. o. atromaculatum* occur in the same streams or river systems throughout much of their range. Cole (1957) stated that the differentiation of these forms seems to be the result of differences in ecological preferences. He also reported a situation which seems to closely parallel part of the possible evolutionary history of *E. longimanum* and *E. podostemone*. In the Rappahannock River, in addition to *E. o. atromaculatum* and *E. o. olmstedi*, Cole found an upstream population which was subspecifically differentiated from *E. o. olmstedi* and *E. o. atromaculatum*. This subspecies, *E. o. vexillare*, still retained genetic contact with *E. o. olmstedi* through a zone of intergradation. This could have possibly been the situation in the James and Roanoke Rivers before the introduction of *E. nigrum* stock, which provided the competitional force necessary to halt gene flow between the adjacent populations.

SUMMARY

Etheostoma longimanum, the Longfin Darter, an endemic species of the James River system of Virginia and West Virginia, is compared to E. podostemone, the Riverweed Darter, an endemic species of the Roanoke River system in Virginia and North Carolina. The marked similarity of these two forms has led to some doubt as to whether they were specifically distinct from each other.

These two forms have differentiated from each other on the specific or intermediate specific level in seven morphological characters. Subspecific differences were found to occur in seven other characters. These differences, as well as additional qualitative differences, show a distinct separation between the two forms, and are interpreted by the writer as evidence that E. longimanum and E. podostemone represent valid species.

The origins of these two species seems best explained by speciation in the two separate river systems from E. olmstedi stock, populations that are presently recognized as E. olmstedi olmstedi. This differentiation probably began as separation into upstream and downstream stocks, with subsequent divergence being enhanced by introduction of E. nigrum into both river systems by stream captures from the New River.

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Table 1. Scales in lateral line

Number of scales	*E. longimanum*	*E. podostemone*
35	0	1
36	0	4
37	0	21
38	0	35
39	0	31
40	3	19
41	5	14
42	9	0
43	8	0
44	14	0
45	21	0
46	16	0
47	6	0
48	0	0
49	1	0
N	83	125
$\bar{x}$	44.3	38.6
s	1.9	1.4
$s_{\bar{x}}$	0.21	0.12

Table 2. Scale rows above lateral line to origin of second dorsal fin

Number of scale rows	*E. longimanum*	*E. podostemone*
4	0	1
5	8	111
6	72	14
7	3	0
N	83	126
$\bar{x}$	5.9	5.1
s	0.4	0.3
$s_{\bar{x}}$	0.04	0.03

Table 3. Scale rows above lateral line to origin of first dorsal fin

Number of scale rows	*E. longimanum*	*E. podostemone*
3	0	1
4	43	108
5	40	17
N	83	126
$\bar{x}$	4.5	4.1
s	0.5	0.4
$s_{\bar{x}}$	0.05	0.03

Table 4. Scale rows below lateral line to origin of anal fin

Number of scale rows	*E. longimanum*	*E. podostemone*
5	0	5
6	2	52
7	39	58
8	37	10
9	5	0
N	83	125
$\bar{x}$	7.5	6.6
s	0.6	0.7
$s_{\bar{x}}$	0.07	0.06

Table 5. Scale rows around caudal peduncle

Number of scale rows	*E. longimanum*	*E. podostemone*
14	0	2
15	3	14
16	14	96
17	39	12
18	26	2
19	1	0
N	83	126
$\bar{x}$	17.1	16.0
s	0.8	0.6
$s_{\bar{x}}$	0.09	0.05

Table 6. Lateral scale rows from origin of first dorsal fin to origin of second dorsal fin

Number of scale rows	*E. longimanum*	*E. podostemone*
11	0	1
12	0	12
13	0	37
14	1	25
15	15	6
16	26	0
17	29	0
18	9	0
N	80	80
$\bar{x}$	16.4	13.5
s	1.0	0.9
$s_{\bar{x}}$	0.10	0.10

Table 7. Scale rows around caudal peduncle plus scales above lateral line to origin of second dorsal fin plus scales below lateral line to origin of anal fin

Number of scale rows	*E. longimanum*	*E. podostemone*
24	0	1
25	0	2
26	0	13
27	1	39
28	5	49
29	9	14
30	19	4
31	31	3
32	11	0
33	6	0
N	82	125
$\bar{x}$	30.6	27.6
s	1.3	1.2
$s_{\bar{x}}$	0.14	0.10

Table 8. Spines in first dorsal fin

Number of spines	*E. longimanum*	*E. podostemone*
8	0	10
9	25	80
10	51	36
11	6	1
N	82	127
$\bar{x}$	9.8	9.2
s	0.6	0.6
$s_{\bar{x}}$	0.06	0.05

Table 9. Rays in second dorsal fin

Number of rays	*E. longimanum*	*E. podostemone*
10	0	1
11	19	4
12	57	71
13	5	48
14	1	3
N	82	127
$\bar{x}$	11.9	12.4
s	0.6	0.6
$s_{\bar{x}}$	0.06	0.06

Table 10. Rays in anal fin

Number of rays	*E. longimanum*	*E. podostemone*
5	0	1
6	3	81
7	57	45
8	22	1
N	82	128
$\bar{x}$	7.2	6.4
s	0.5	0.5
$s_{\bar{x}}$	0.06	0.04

Table 11. Rays in left pectoral fin

Number of rays	*E. longimanum*	*E. podostemone*
10	0	1
11	0	5
12	4	106
13	60	14
14	17	0
N	81	126
$\bar{x}$	13.2	12.1
s	0.5	0.4
$s_{\bar{x}}$	0.05	0.04

Table 12. Rays in right pectoral fin

Number of rays	*E. longimanum*	*E. podostemone*
10	0	1
11	0	4
12	1	108
13	63	13
14	17	0
N	81	126
$\bar{x}$	13.2	12.1
s	0.4	0.41
$s_{\bar{x}}$	0.04	0.03

Table 13. Pores in infraorbital canal

Number of pores	*E. longimanum*	*E. podostemone*
7	6	6
8	86	84
9	11	10
N	103	100
$\bar{x}$	8.0	8.0
s	0.4	0.4
$s_{\bar{x}}$	0.04	0.04

Table 14. Pores in preoperculomandibular canal

Number of pores	*E. longimanum*	*E. podostemone*
8	0	4
9	9	81
10	93	17
11	0	1
N	102	103
$\bar{x}$	9.9	9.1
s	0.3	0.5
$s_{\bar{x}}$	0.03	0.05

Table 15. Body depth in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
15.5-15.7	0	1
15.8-16.0	0	0
16.1-16.3	0	0
16.4-16.6	0	2
16.7-16.9	3	1
17.0-17.2	1	7
17.3-17.5	5	6
17.6-17.8	5	11
17.9-18.1	7	14
18.2-18.4	11	16
18.5-18.7	9	10
18.8-19.0	9	11
19.1-19.3	6	8
19.4-19.6	6	4
19.7-19.9	6	0
20.0-20.2	2	1
20.3-20.5	1	0
20.6-20.8	1	0
N	72	92
$\bar{x}$	18.6	18.2
s	0.9	0.8
$s_{\bar{x}}$	0.10	0.08

Table 16. Caudal peduncle depth in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
8.8-9.0	2	0
9.1-9.3	1	0
9.4-9.6	5	0
9.7-9.9	10	1
10.0-10.2	13	5
10.3-10.5	20	7
10.6-10.8	13	15
10.9-11.1	7	20
11.2-11.4	1	24
11.5-11.7	0	13
11.8-12.0	0	7
N	72	93
$\bar{x}$	10.3	11.1
s	0.5	0.5
$s_{\bar{x}}$	0.06	0.05

Table 17. Head depth in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
14.4-14.6	2	0
14.7-14.9	1	1
15.0-15.2	5	7
15.3-15.5	5	19
15.6-15.8	5	27
15.9-16.1	13	14
16.2-16.4	8	17
16.5-16.7	10	7
16.8-17.0	6	1
17.1-17.3	12	0
17.4-14.6	1	0
17.7-17.9	3	0
18.0-18.2	0	0
18.3-18.5	1	0
N	72	93
$\bar{x}$	16.3	15.8
s	0.8	0.4
$s_{\bar{x}}$	0.10	0.04

Table 18. Head length in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
22.7-22.9	0	1
23.0-23.2	0	0
23.3-23.5	2	2
23.6-23.8	0	9
23.9-24.1	2	16
24.2-24.4	9	16
24.5-24.7	5	14
24.8-25.0	12	9
25.1-25.3	6	13
25.4-25.6	6	4
25.7-25.9	12	4
26.0-26.2	4	2
26.3-26.5	5	1
26.6-26.8	5	0
26.9-27.1	1	0
27.2-27.4	1	2
27.5-27.7	0	0
27.8-28.0	0	0
28.1-28.3	1	0
N	71	93
$\bar{x}$	25.4	24.6
s	0.9	0.8
$s_{\bar{x}}$	0.11	0.08

Table 19. Snout length in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
4.7-4.9	0	6
5.0-5.2	0	18
5.3-5.5	3	32
5.6-5.8	8	20
5.9-6.1	11	13
6.2-6.4	21	4
6.5-6.7	18	0
6.8-7.0	7	0
7.1-7.3	2	0
7.4-7.6	1	0
N	71	93
$\bar{x}$	6.3	5.4
s	0.4	0.4
$s_{\bar{x}}$	0.05	0.04

Table 20. Postorbital head length in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
12.3-12.5	1	3
12.6-12.8	5	4
12.9-13.1	10	11
13.2-13.4	13	15
13.5-13.7	12	26
13.8-14.0	18	17
14.1-14.3	5	9
14.4-14.6	4	5
14.7-14.9	2	1
15.0-15.2	1	0
15.3-15.5	0	1
N	71	92
$\bar{x}$	13.6	13.6
s	0.5	0.5
$s_{\bar{x}}$	0.07	0.05

Table 21. Length of longest pectoral fin ray in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
24.7-25.3	0	1
25.4-26.0	1	0
26.1-26.7	0	1
26.8-27.4	0	1
27.5-28.1	2	2
28.2-28.8	3	5
28.9-29.5	3	15
29.6-30.2	6	24
30.3-30.9	11	19
31.0-31.6	13	31
31.7-32.3	7	20
32.4-33.0	7	9
33.1-33.7	13	3
33.8-34.4	11	2
34.5-35.1	11	2
35.2-35.8	6	0
35.9-36.5	8	0
36.6-37.2	5	0
37.3-37.9	1	0
38.0-38.6	0	0
38.7-39.3	1	0
N	109	135
$\bar{x}$	32.9	30.8
s	2.4	1.5
$s_{\bar{x}}$	0.23	0.13

Table 22. Length of longest pelvic fin ray in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
18.7-19.1	0	1
19.2-19.6	0	1
19.7-20.1	1	5
20.2-20.6	0	8
20.7-21.1	0	9
21.2-21.6	0	15
21.7-22.1	2	16
22.2-22.6	8	17
22.7-23.1	10	11
23.2-23.6	10	7
23.7-24.1	12	2
24.2-24.6	11	1
24.7-25.1	9	0
25.2-25.6	2	0
25.7-26.1	1	0
26.2-26.6	3	0
26.7-27.1	2	0
27.2-27.6	1	0
N	72	93
$\bar{x}$	23.9	21.8
s	1.3	1.1
$s_{\bar{x}}$	0.15	0.11

Table 23. Length of first dorsal fin base in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
24.2-24.5	0	6
24.6-24.9	4	1
25.0-25.3	4	6
25.4-25.7	2	10
25.8-26.1	2	7
26.2-26.5	8	16
26.6-26.9	11	14
27.0-27.3	15	15
27.4-27.7	13	19
27.8-28.1	13	7
28.2-28.5	9	14
28.6-28.9	9	7
29.0-29.3	8	5
29.4-29.7	4	1
29.8-30.1	6	4
30.2-30.5	1	3
30.6-30.9	1	0
N	110	135
$\bar{x}$	27.7	27.2
s	1.3	1.4
$s_{\bar{x}}$	0.13	0.12

Table 24. Length of depressed second dorsal fin of females in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
26.4-26.8	2	0
26.9-27.3	1	0
27.4-27.8	2	0
27.9-28.3	0	2
28.4-28.8	5	4
28.9-29.3	8	5
29.4-29.8	6	6
29.9-30.3	13	8
30.4-30.8	4	12
30.9-31.3	5	11
31.4-31.8	5	8
31.9-32.3	7	2
32.4-32.8	1	2
32.9-33.3	0	0
33.4-33.8	1	0
N	60	60
$\bar{x}$	30.1	30.4
s	1.5	1.1
$s_{\bar{x}}$	0.19	0.14

Table 25. Caudal peduncle length in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
24.5-24.7	0	1
24.8-25.0	0	0
25.1-25.3	1	2
25.4-25.6	1	2
25.7-25.9	4	3
26.0-26.2	4	7
26.3-26.5	7	8
26.6-26.8	7	6
26.9-27.1	9	13
27.2-27.4	10	7
27.5-27.7	7	19
27.8-28.0	4	7
28.1-28.3	6	5
28.4-28.6	6	1
28.7-28.9	4	6
29.0-29.2	0	2
29.3-29.5	1	2
29.6-29.8	1	1
N	72	92
$\bar{x}$	27.4	27.3
s	1.0	1.0
$s_{\bar{x}}$	0.11	0.11

Table 26. Predorsal length in standard length

Proportion of measurement	*E. longimanum*	*E. podostemone*
28.6-28.8	0	2
28.9-29.1	0	1
29.2-29.4	0	6
29.5-29.7	0	5
29.8-30.0	2	8
30.1-30.3	1	11
30.4-30.6	1	8
30.7-30.9	5	10
31.0-31.2	3	12
31.3-31.5	4	8
31.6-31.8	6	9
31.9-32.1	10	7
32.2-32.4	9	1
32.5-32.7	7	3
32.8-33.0	10	1
33.1-33.3	7	0
33.4-33.6	4	1
33.7-33.9	0	0
34.0-34.2	3	0
N	72	93
$\bar{x}$	32.4	30.8
s	1.0	1.0
$s_{\bar{x}}$	0.11	0.10

Table 27. Snout length in head length

Proportion measurement	*E. longimanum*	*E. podostemone*
19.3-19.8	0	1
19.9-20.4	0	2
20.5-21.0	0	1
21.1-21.6	1	9
21.7-22.2	5	13
22.3-22.8	2	11
22.9-23.4	6	7
23.5-24.0	8	6
24.1-24.6	11	0
24.7-25.2	6	0
25.3-25.8	7	0
25.9-26.4	0	0
26.5-26.7	1	0
N	50	50
$\bar{x}$	24.1	22.2
s	1.1	0.9
$s_{\bar{x}}$	0.16	0.13

Table 28. Length of orbit in head length

Proportion of measurement	*E. longimanum*	*E. podostemone*
22.2-22.4	0	2
22.5-22.7	0	0
22.8-23.0	0	1
23.1-23.3	0	1
23.4-23.6	0	4
23.7-23.9	1	2
24.0-24.2	2	1
24.3-24.5	5	4
24.6-24.8	4	9
24.9-25.1	1	7
25.2-25.4	8	7
25.5-25.7	6	2
25.8-26.0	2	2
26.1-26.3	1	2
26.4-26.6	4	0
26.7-26.9	5	2
27.0-27.2	3	0
27.3-27.5	2	2
27.6-27.8	1	0
27.9-28.1	3	1
28.2-28.4	1	1
28.5-28.7	1	0
N	50	50
$\bar{x}$	25.9	25.0
s	1.2	1.2
$s_{\bar{x}}$	0.17	0.17

Table 29. Lower jaw length in head length

Proportion of measurement	*E. longimanum*	*E. podostemone*
19.1-19.6	0	1
19.7-20.2	0	1
20.3-20.8	0	0
20.9-21.4	1	5
21.5-22.0	0	8
22.1-22.6	1	12
22.7-23.2	3	14
23.3-23.8	7	8
23.9-24.4	8	1
24.5-25.0	11	0
25.1-25.6	8	0
25.7-26.2	6	0
26.3-26.8	4	0
N	49	50
$\bar{x}$	24.7	22.4
s	1.1	0.9
$s_{\bar{x}}$	0.16	0.13

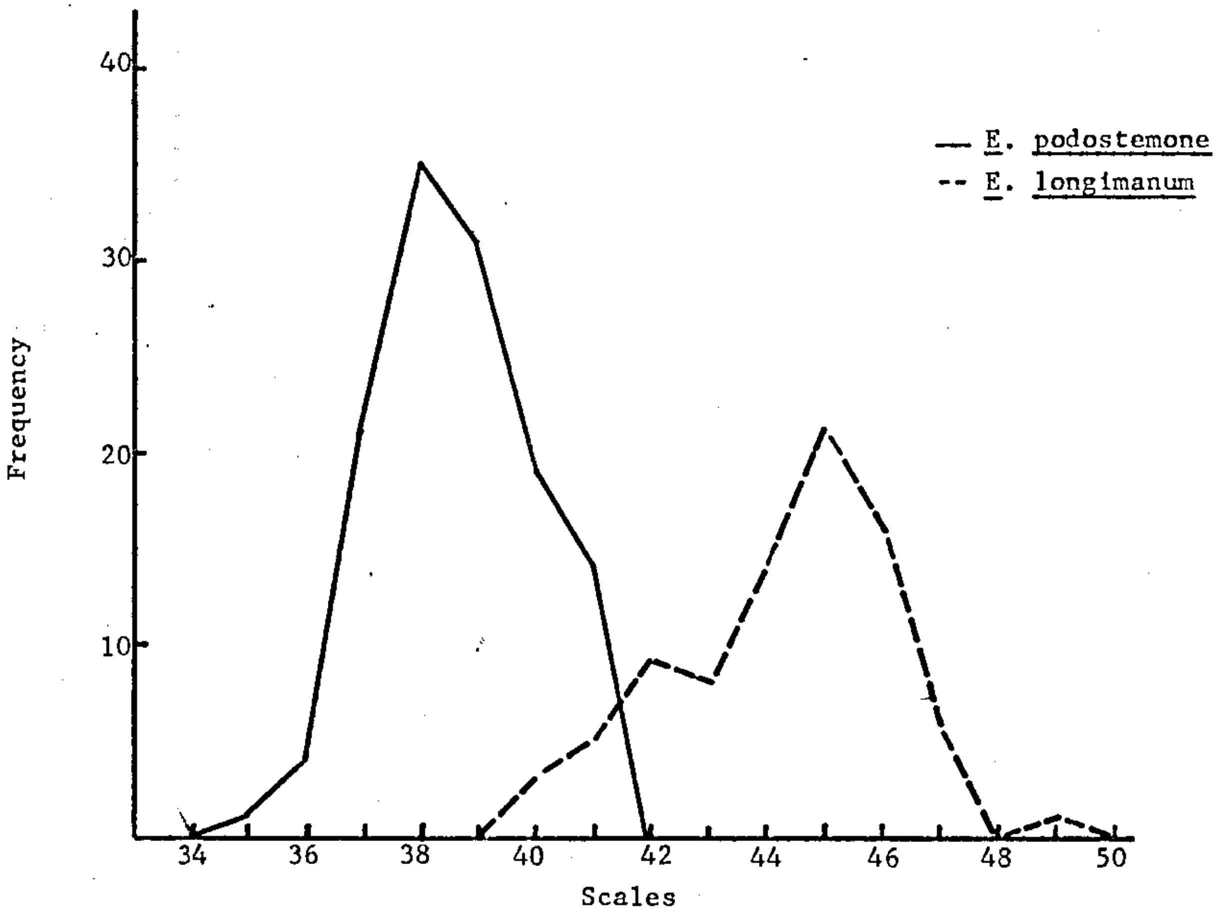


Figure 1. Scales in lateral line

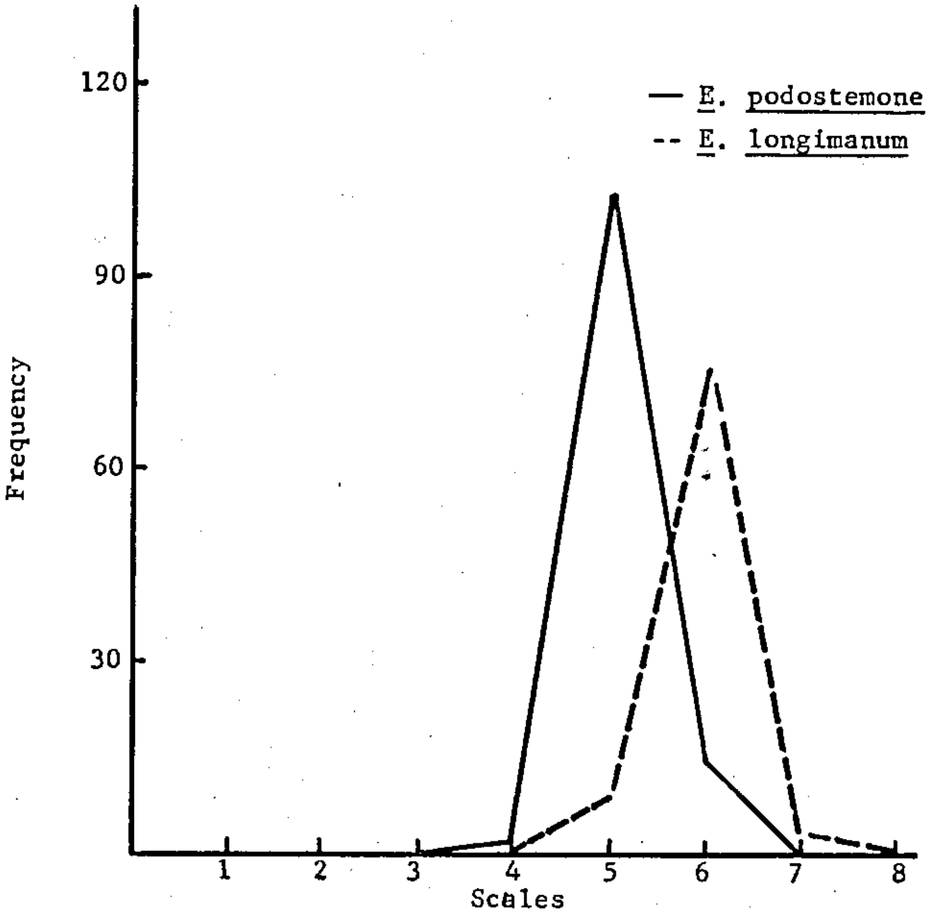


Figure 2. Scale rows above lateral line to origin of second dorsal fin

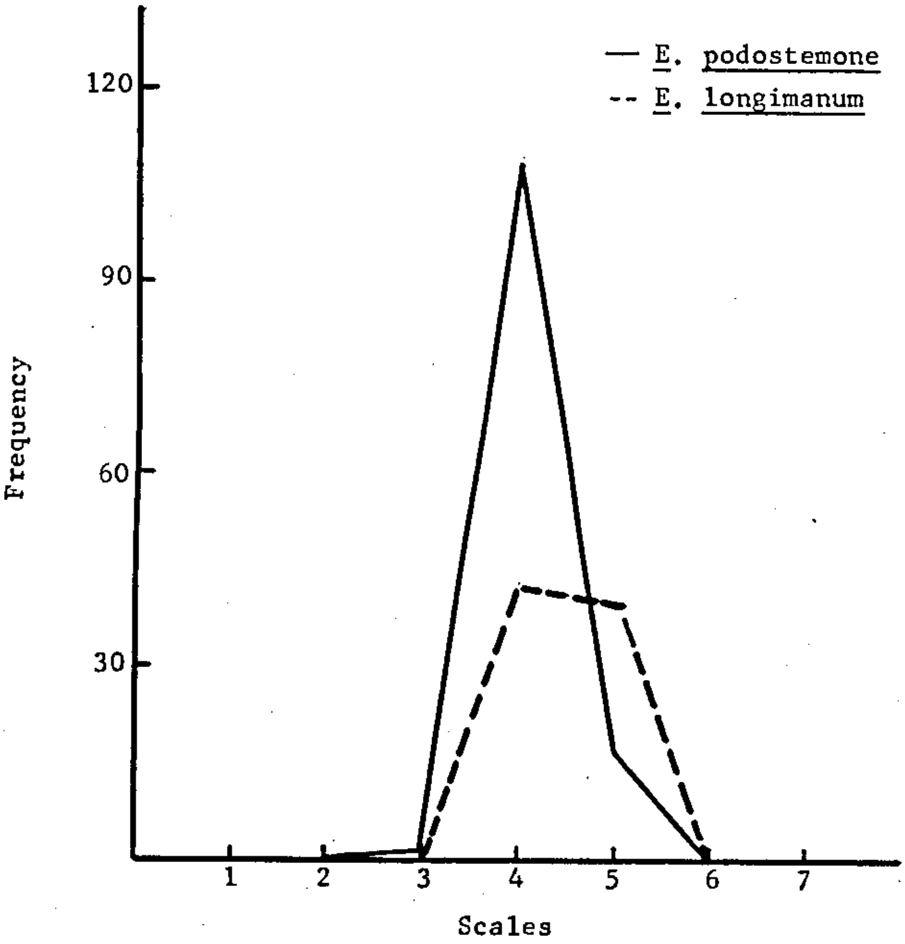


Figure 3. Scale rows above lateral line to origin of first dorsal fin

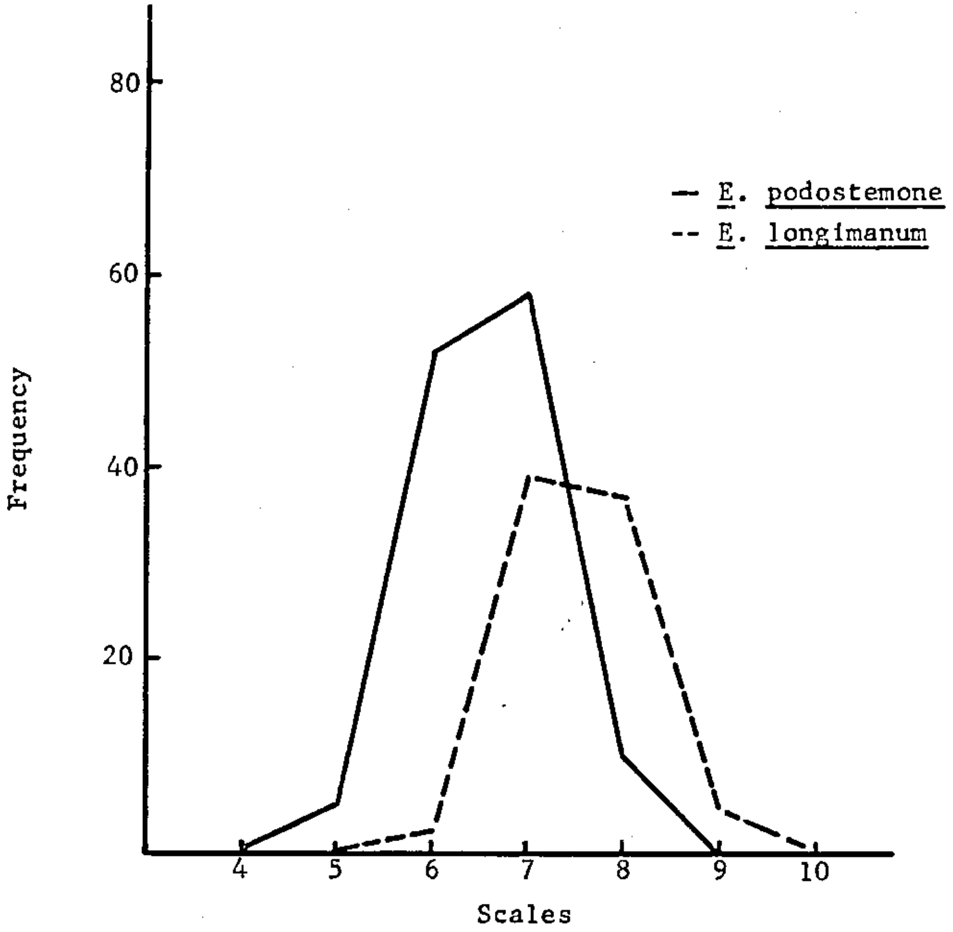


Figure 4. Scale rows below lateral line to origin of anal fin

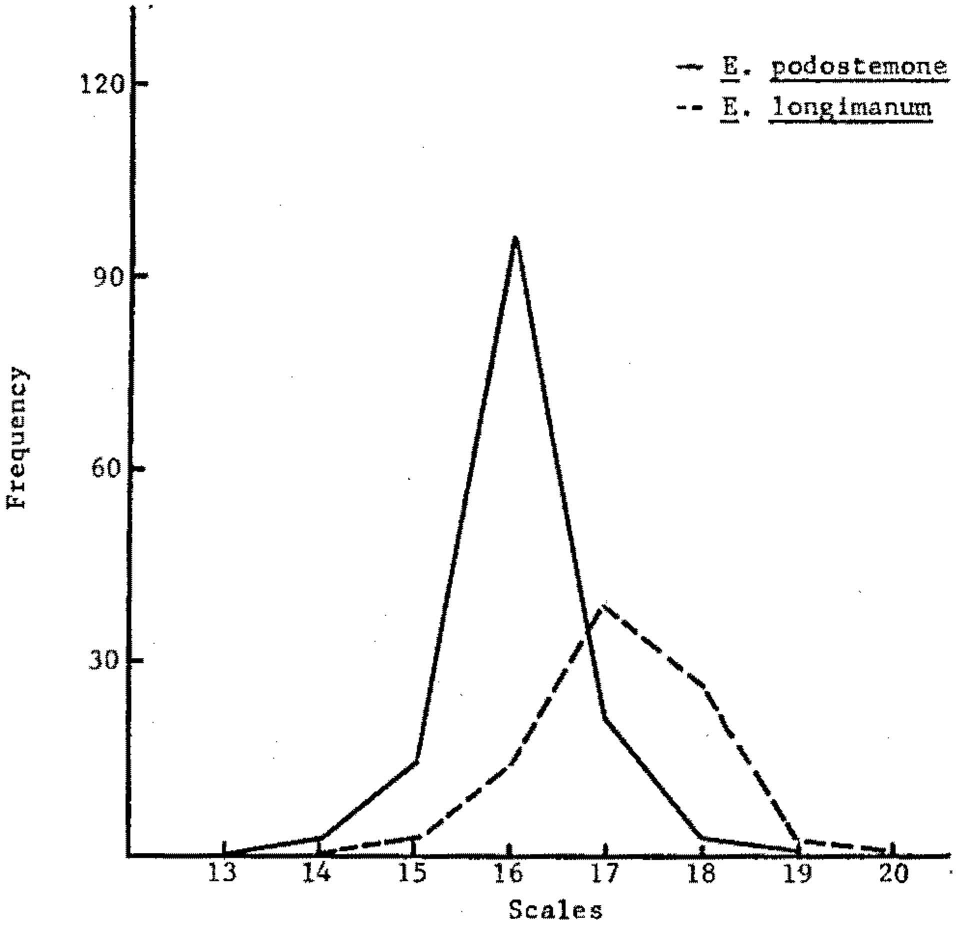


Figure 5. Scale rows around caudal peduncle

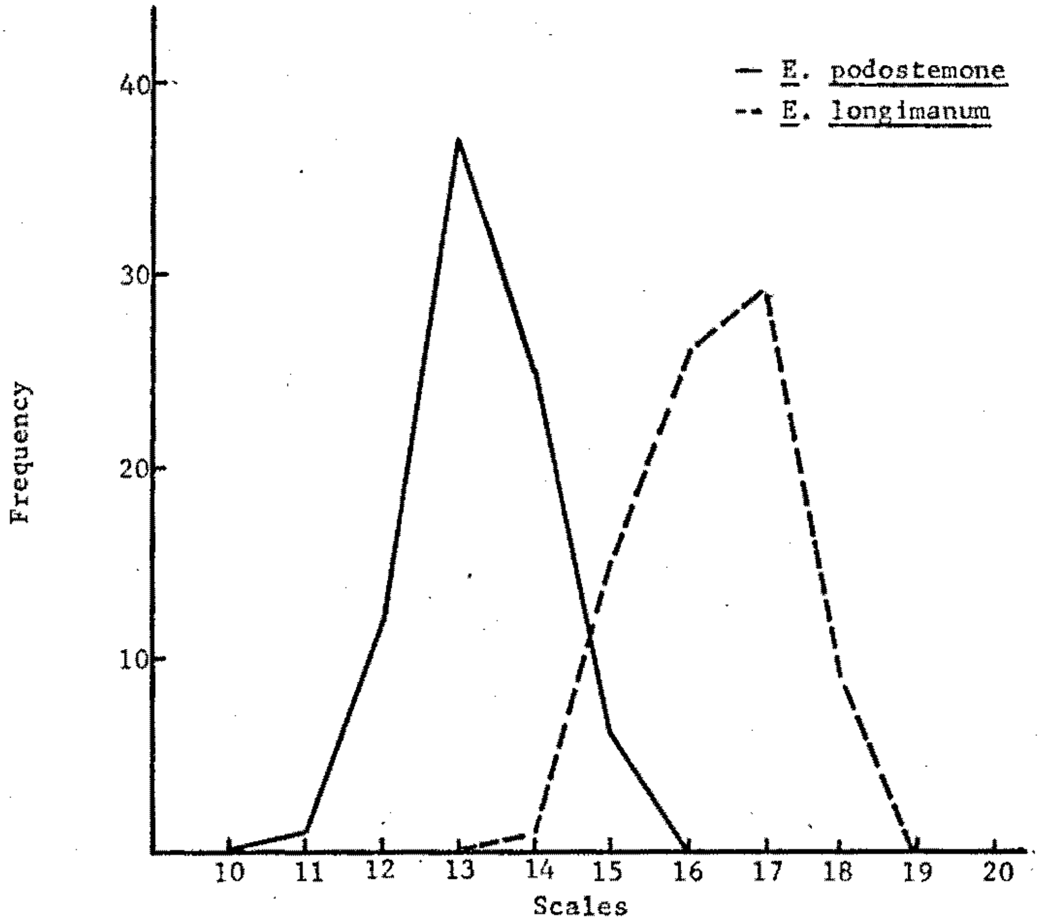


Figure 6. Lateral scale rows from origin of first dorsal fin to origin of second dorsal fin

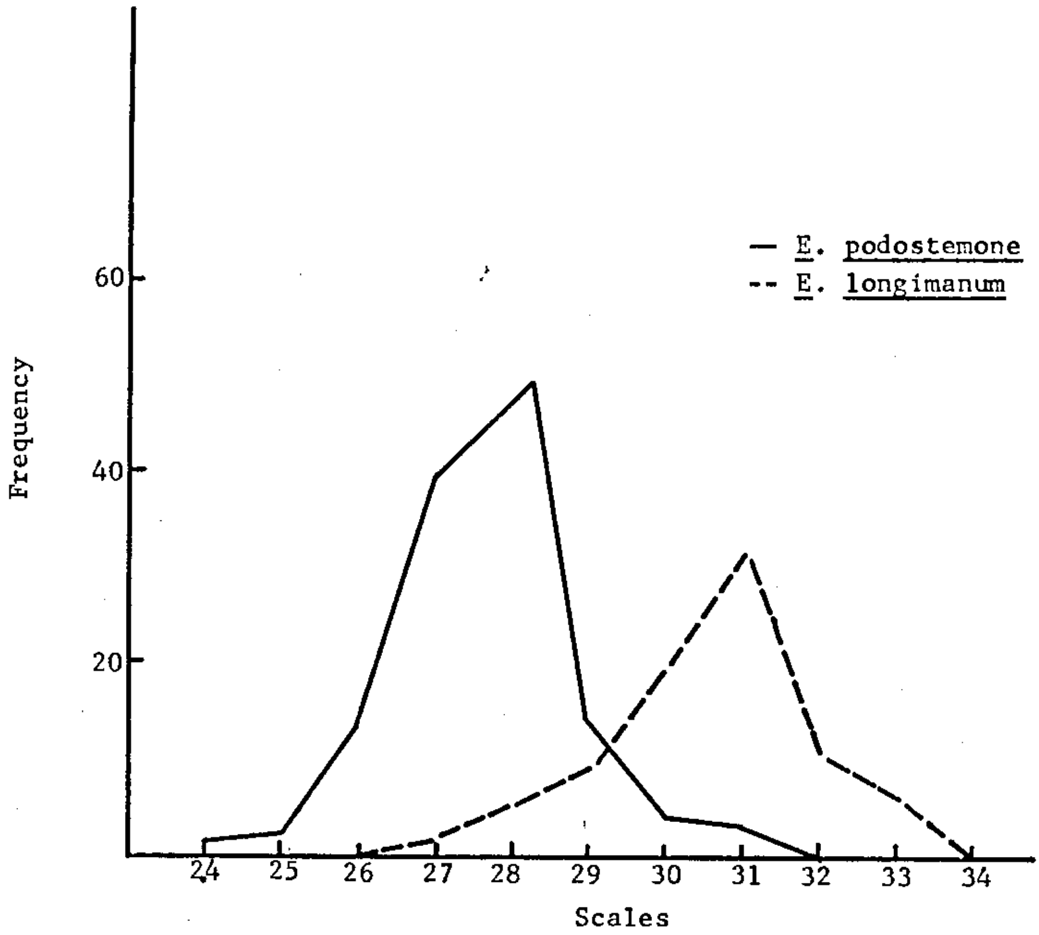


Figure 7. Scale rows around caudal peduncle plus scales above lateral line to origin of second dorsal fin plus scales below lateral line to origin of anal fin

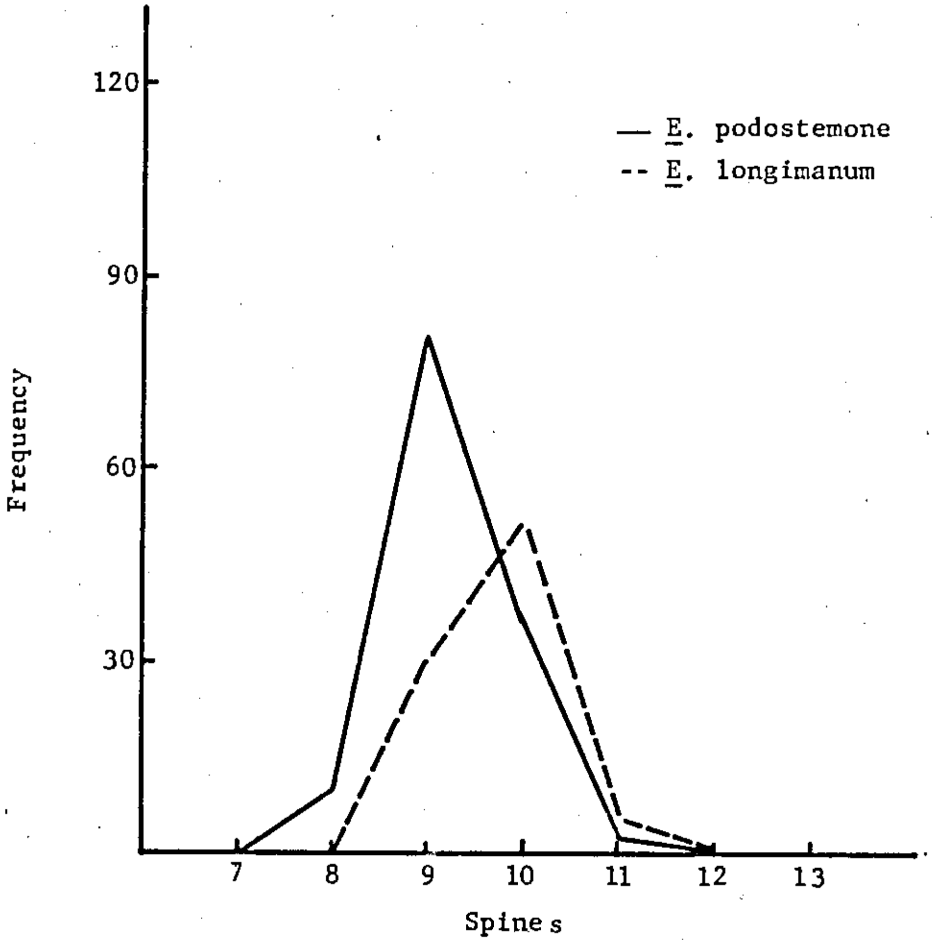


Figure 8. Spines in first dorsal fin

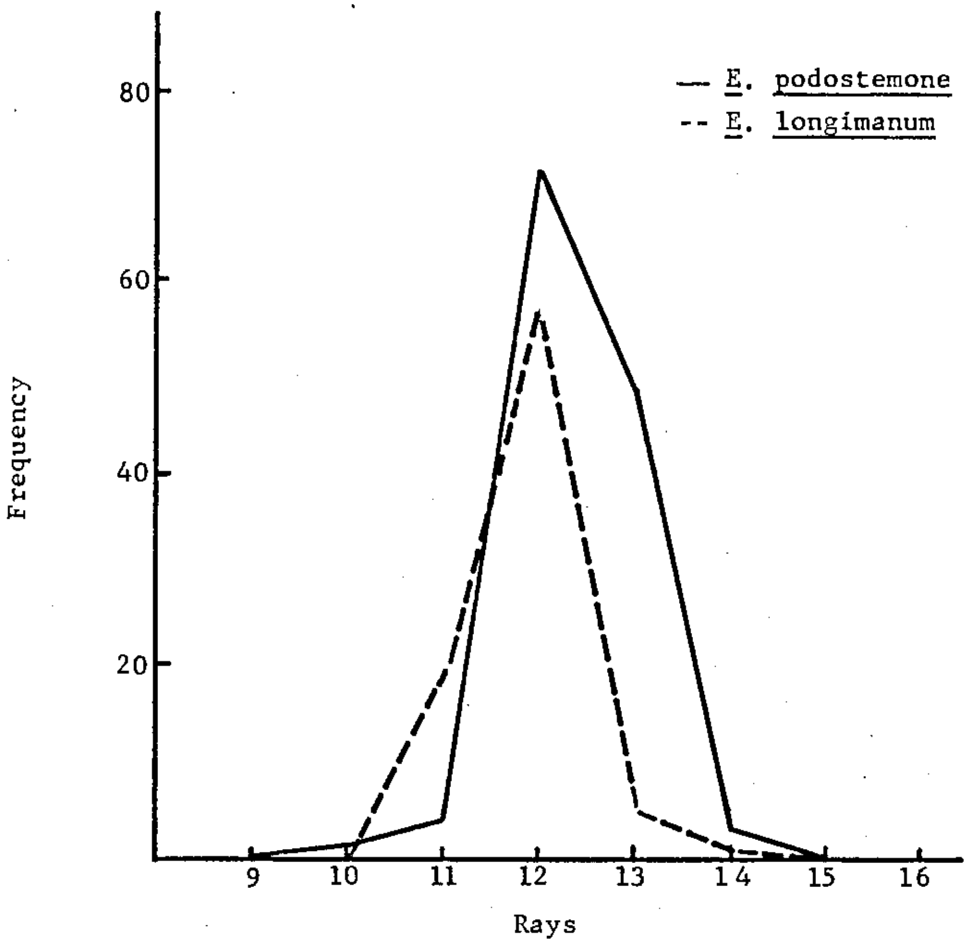


Figure 9. Rays in second dorsal fin

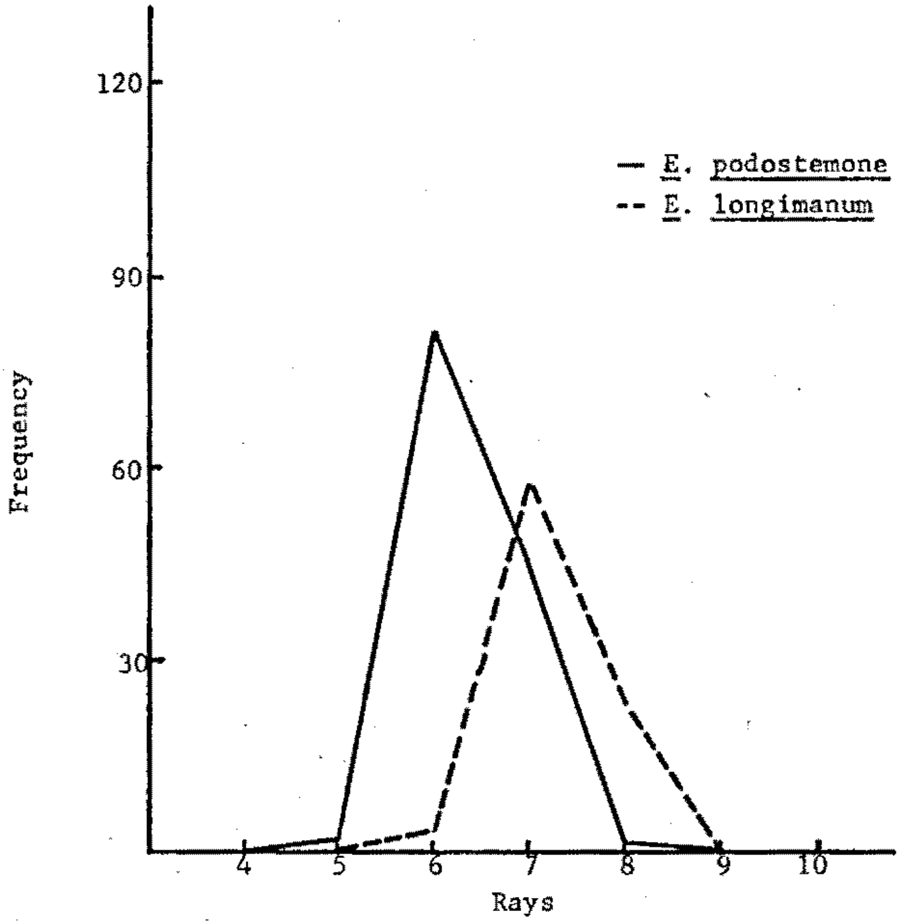


Figure 10. Rays in anal fin

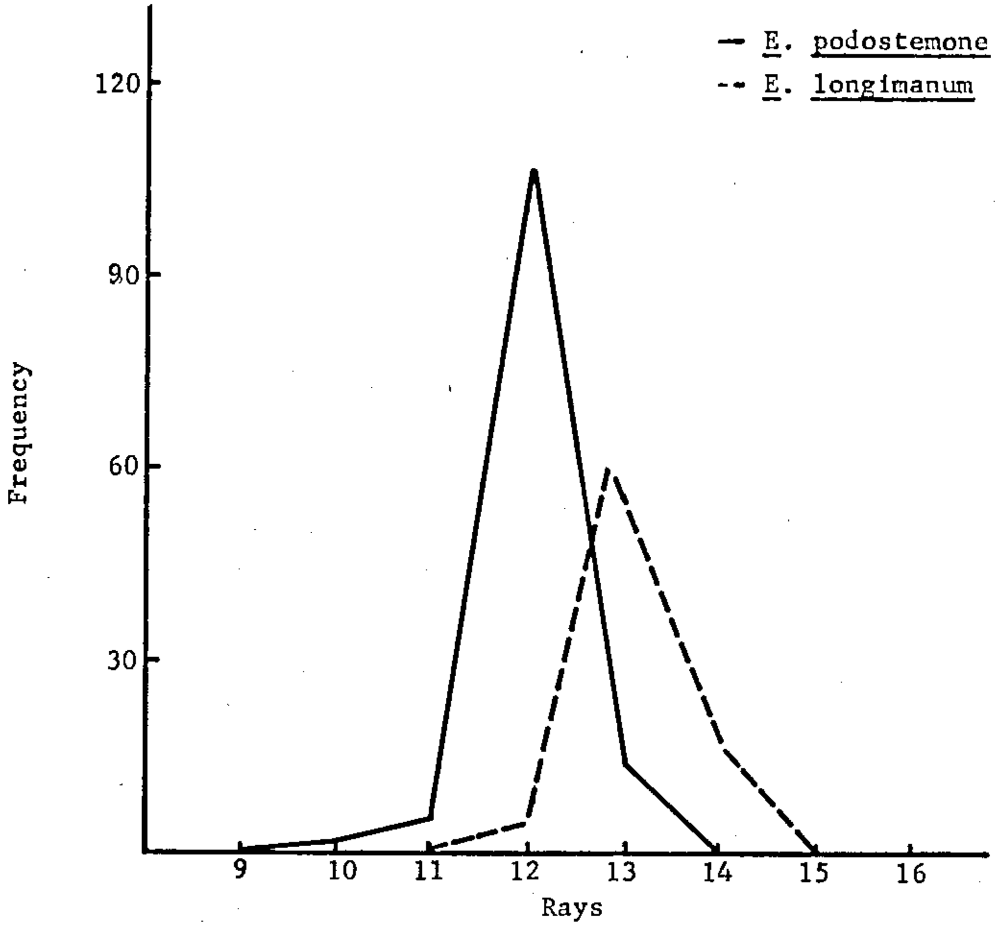


Figure 11. Rays in left pectoral fin

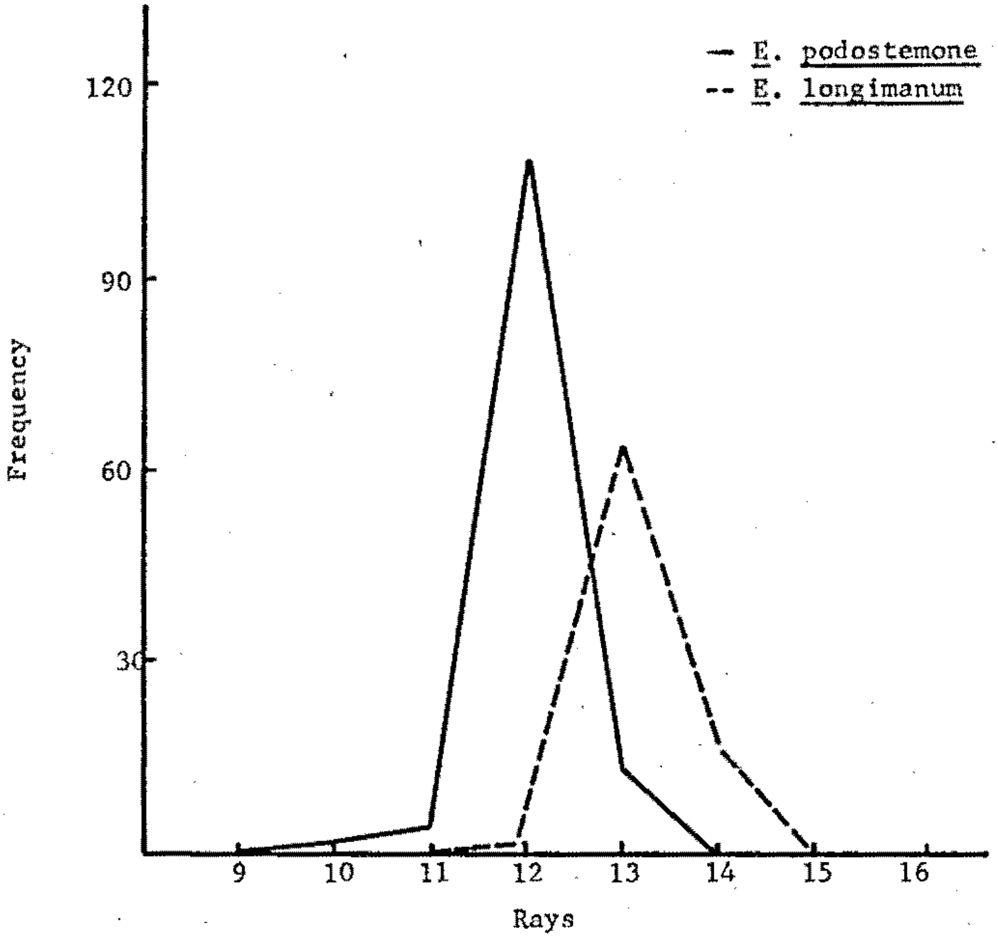


Figure 12. Rays in right pectoral fin

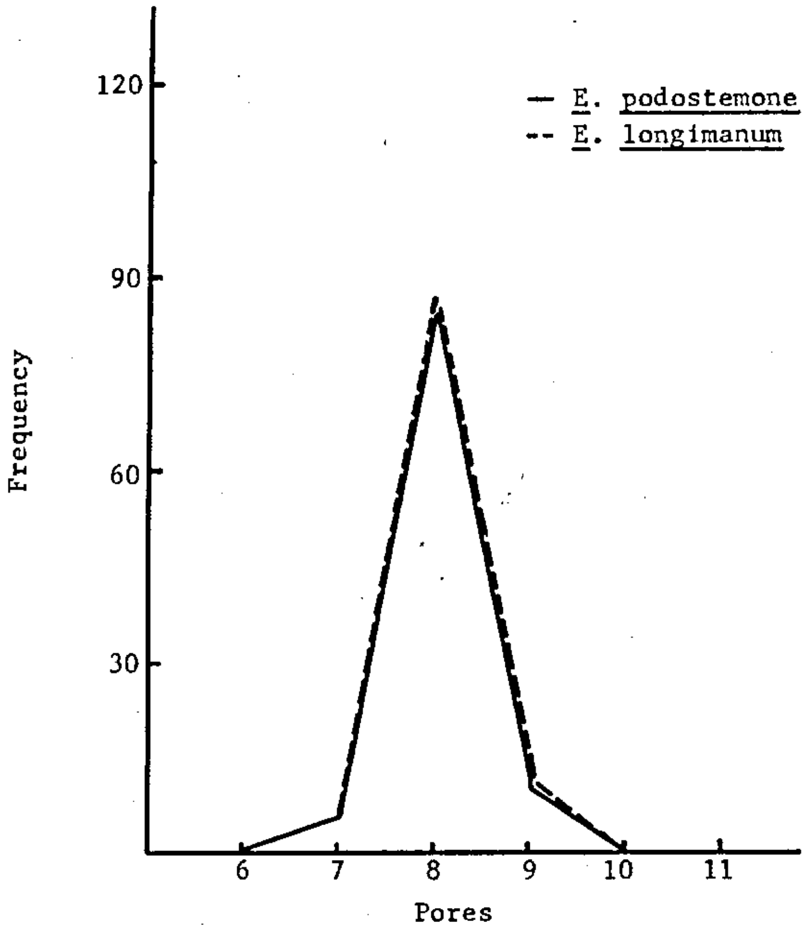


Figure 13. Pores in infraorbital canal

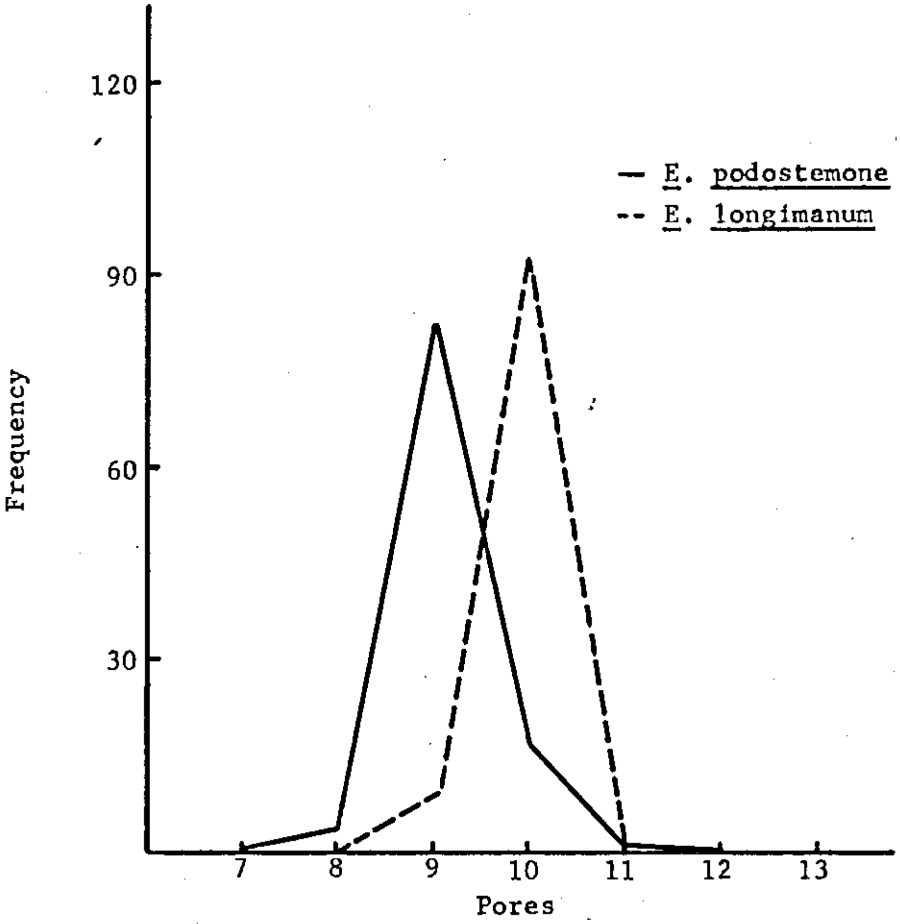


Figure 14. Pores in preoperculomandibular canal

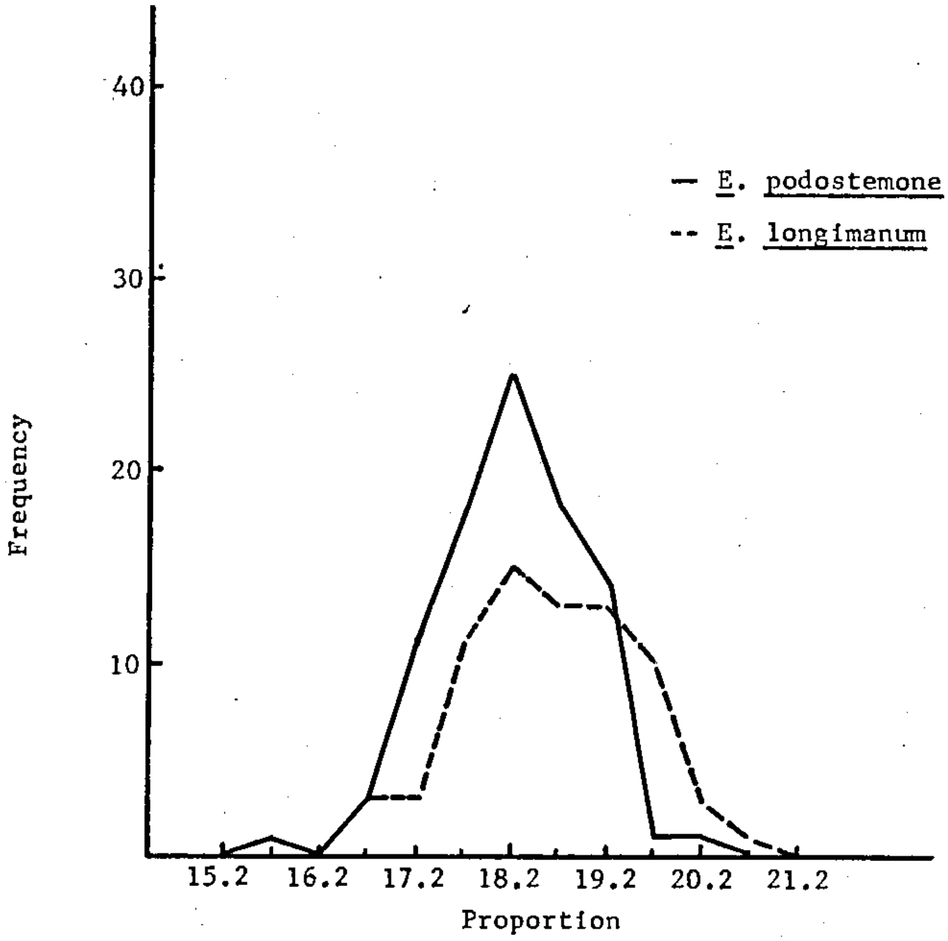


Figure 15. Body depth in standard length

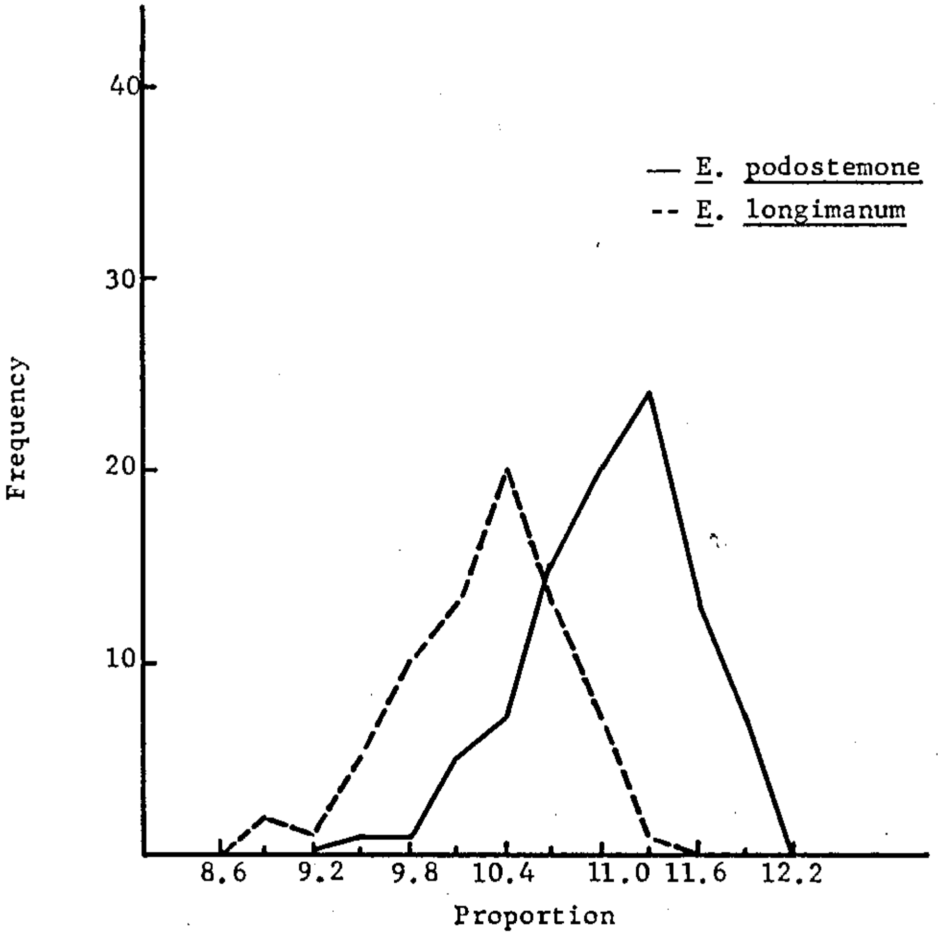


Figure 16. Caudal peduncle depth in standard length

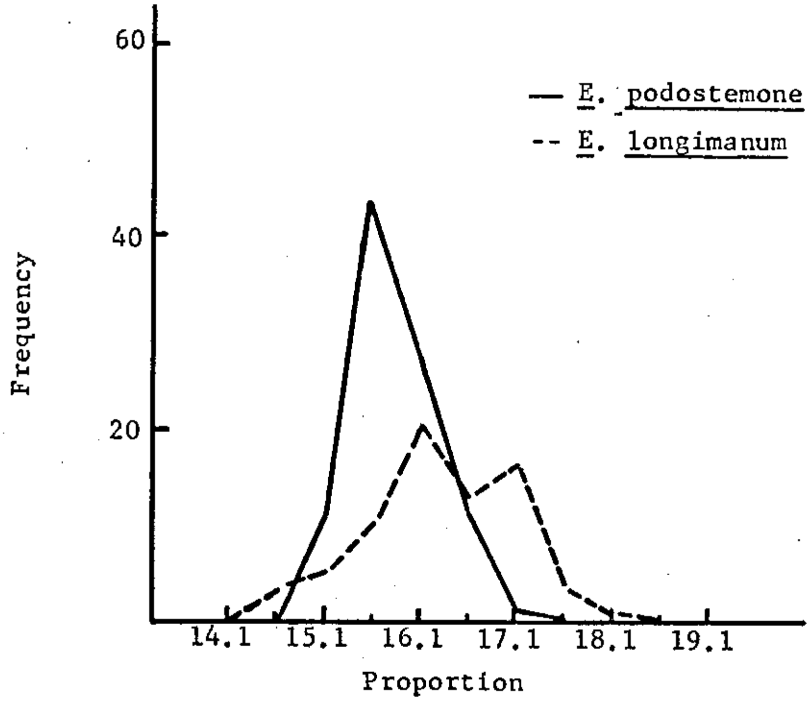


Figure 17. Head depth in standard length

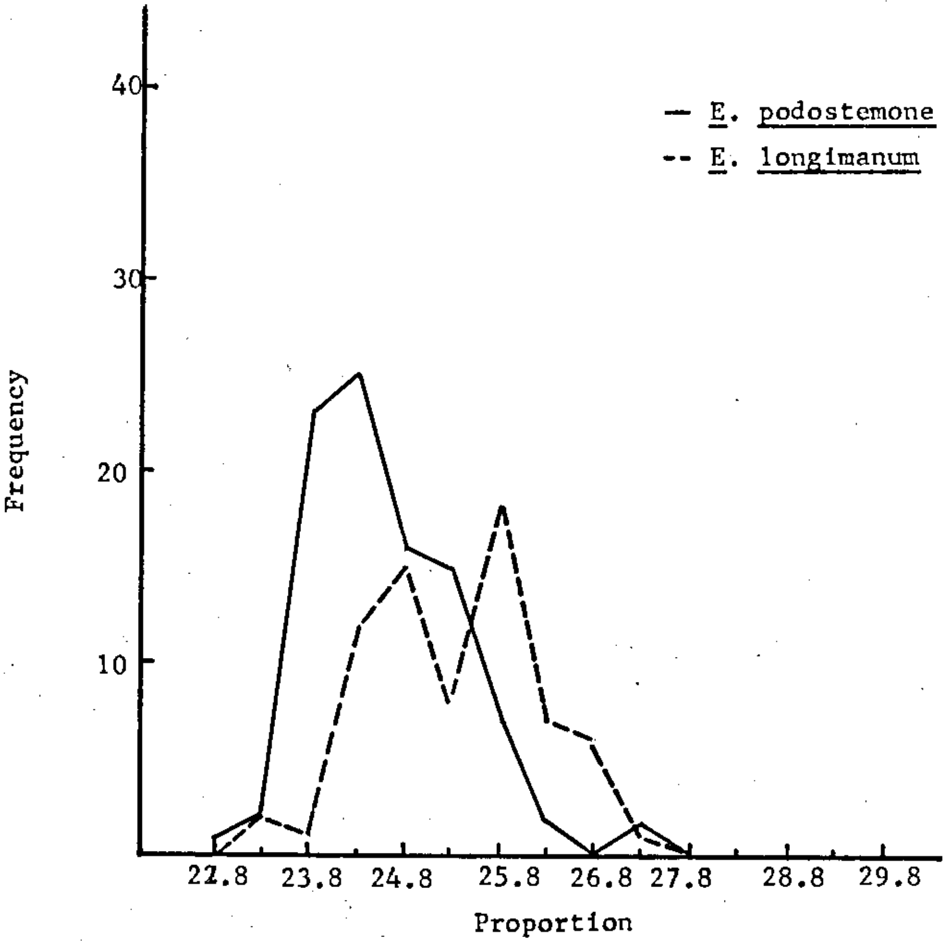


Figure 18. Head length in standard length

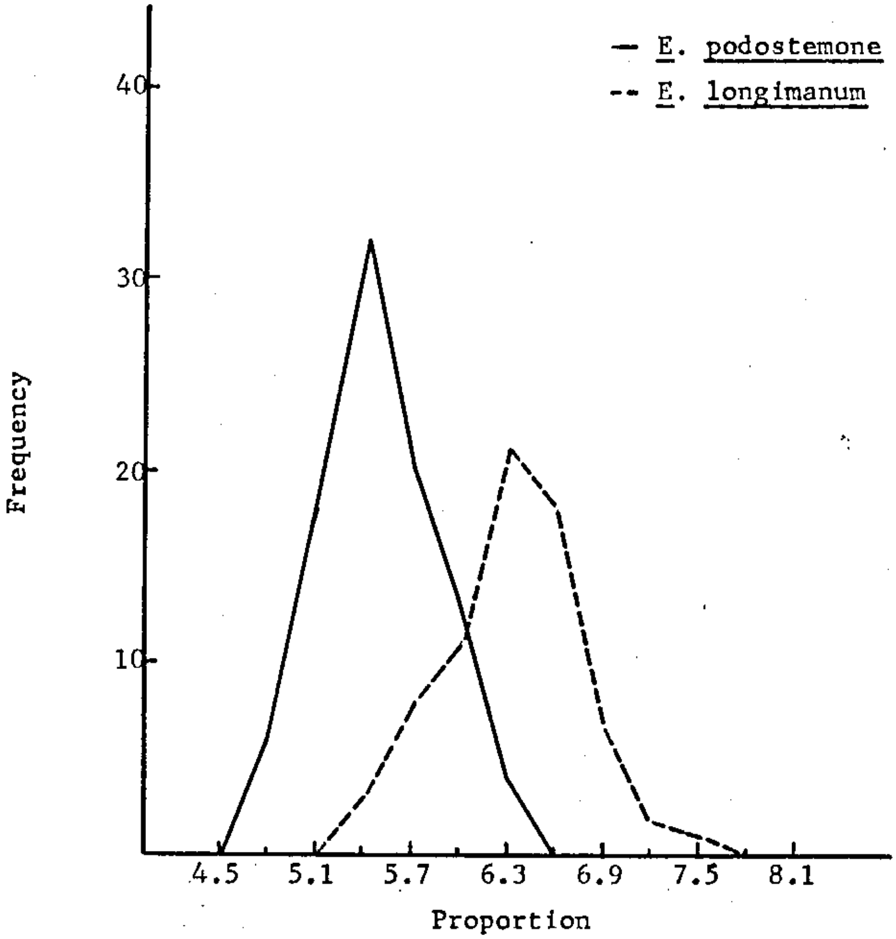


Figure 19. Snout length in standard length

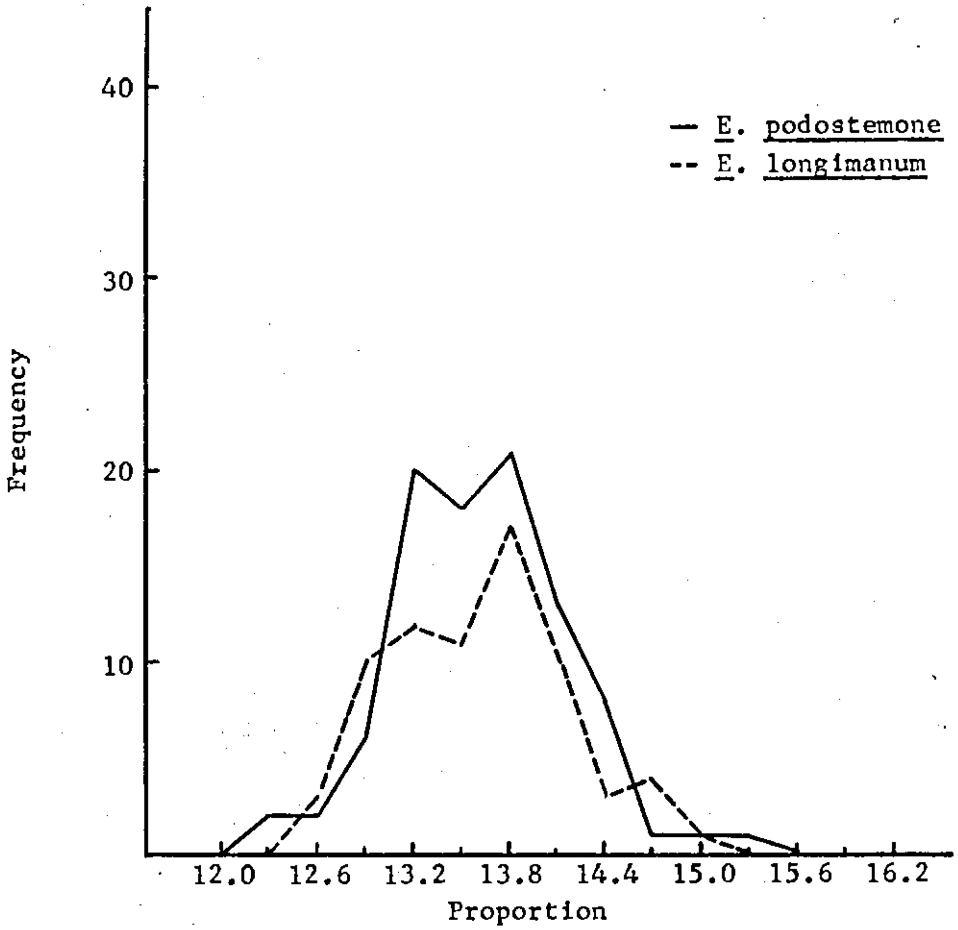


Figure 20. Postorbital head length in standard length

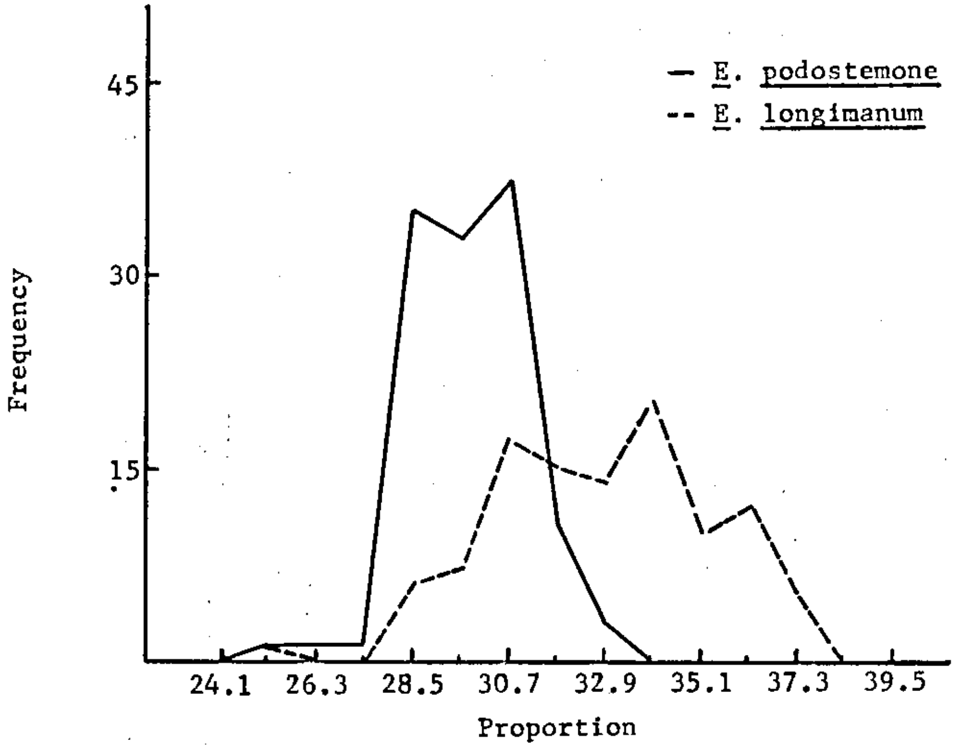


Figure 21. Length of longest pectoral fin ray length in standard length

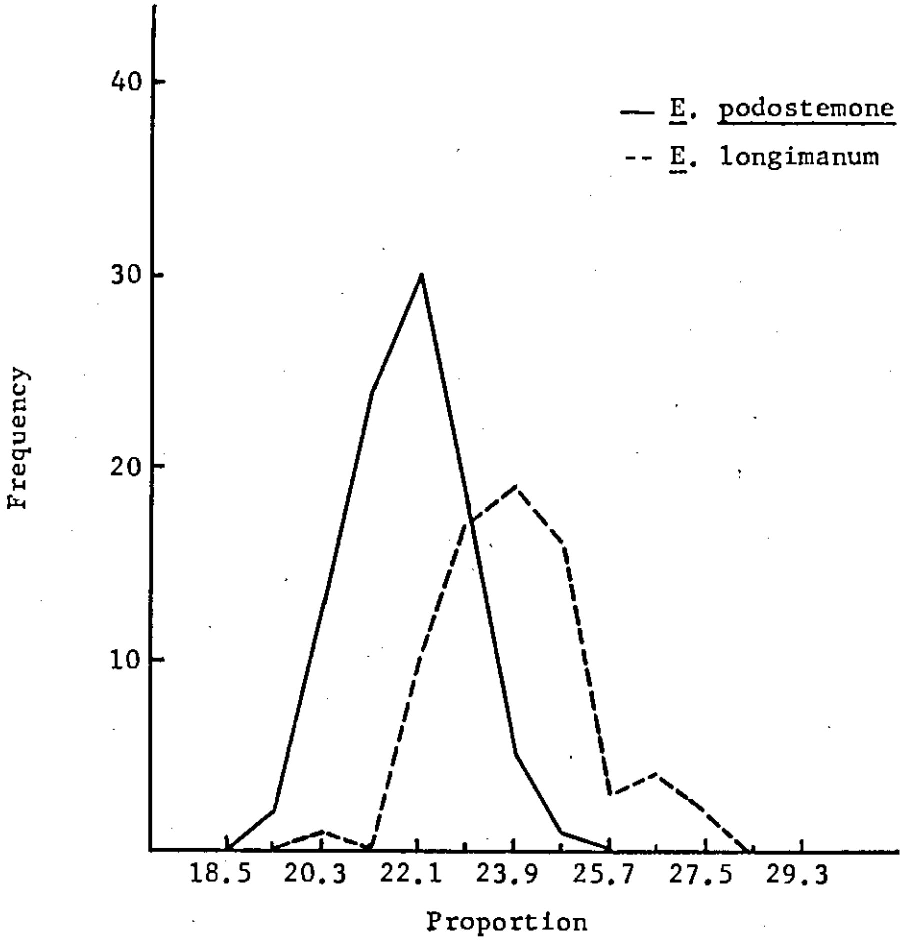


Figure 22. Length of longest pelvic fin ray in standard length

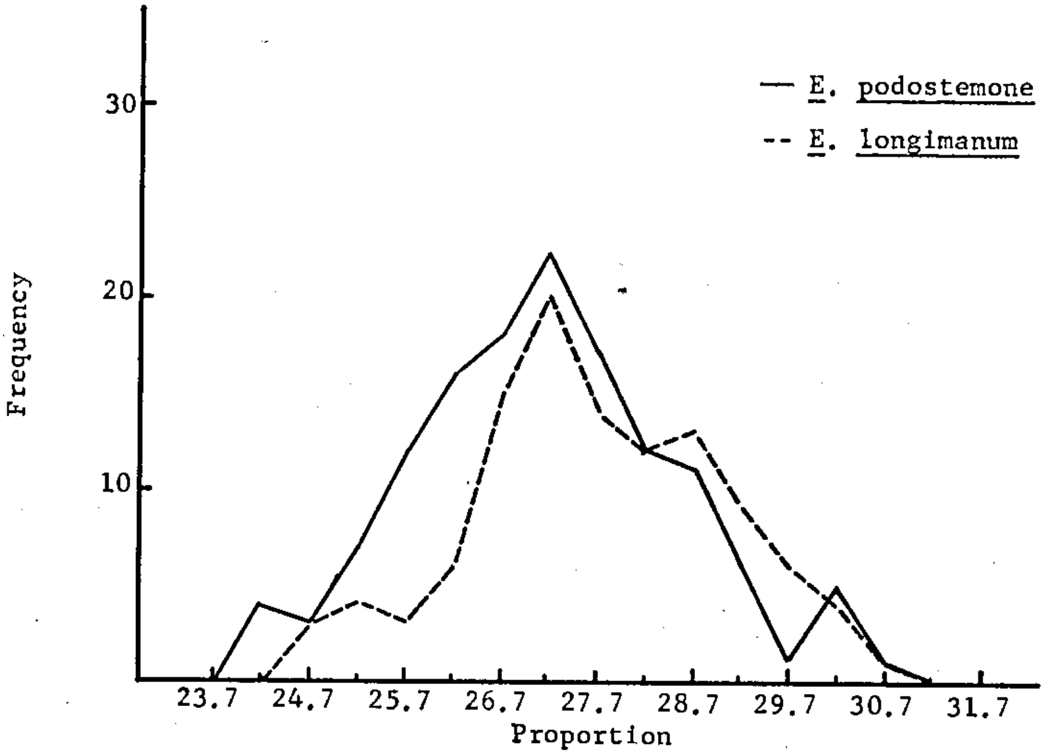


Figure 23. Length of first dorsal fin base in standard length

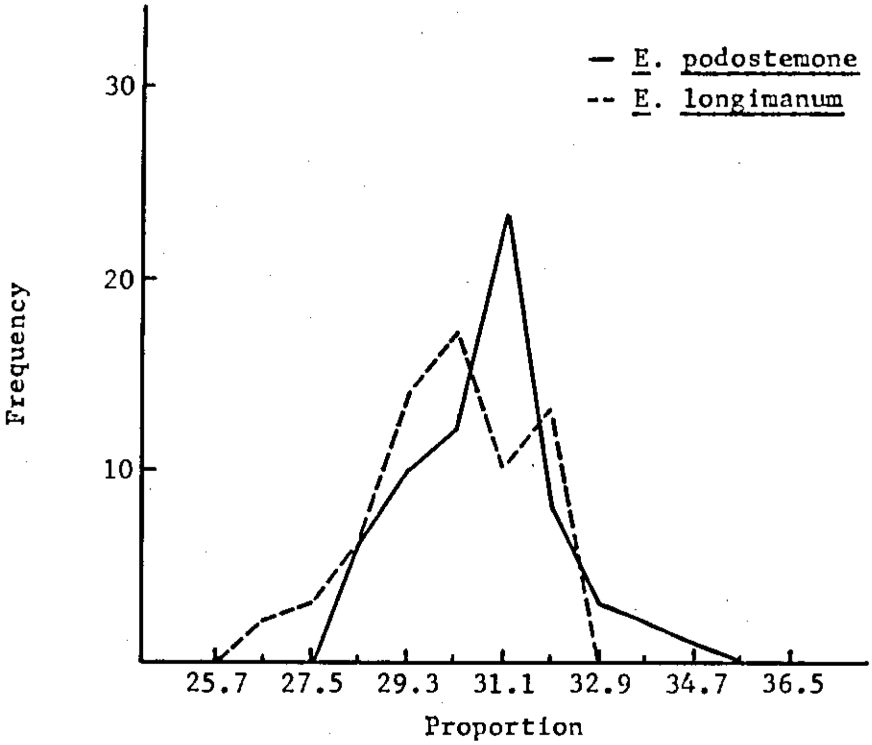


Figure 24. Length of depressed second dorsal fin of females in standard length

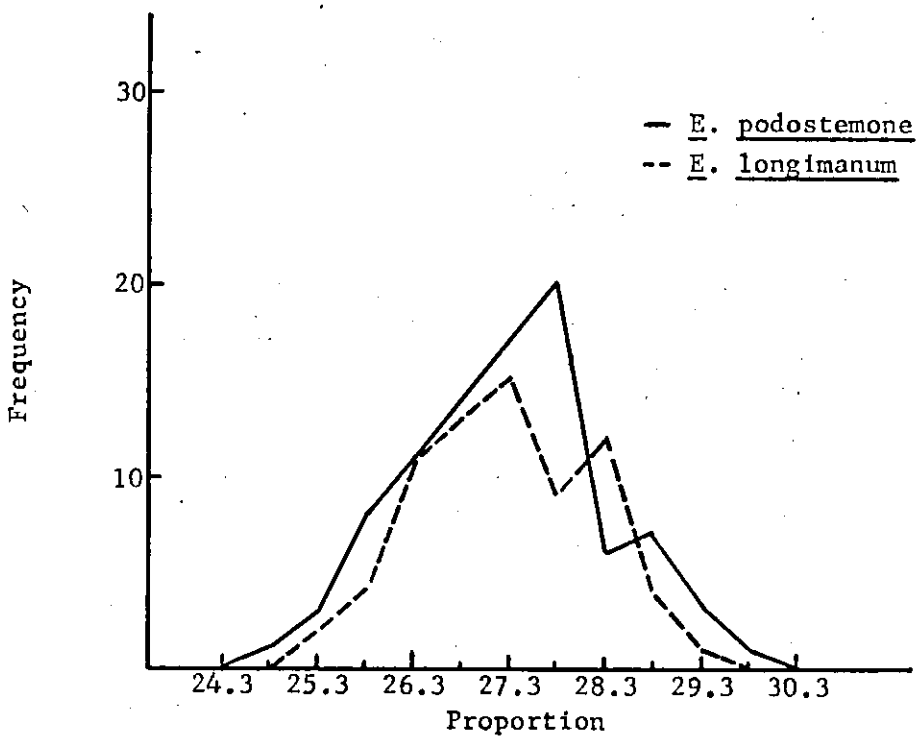


Figure 25. Caudal peduncle length in standard length

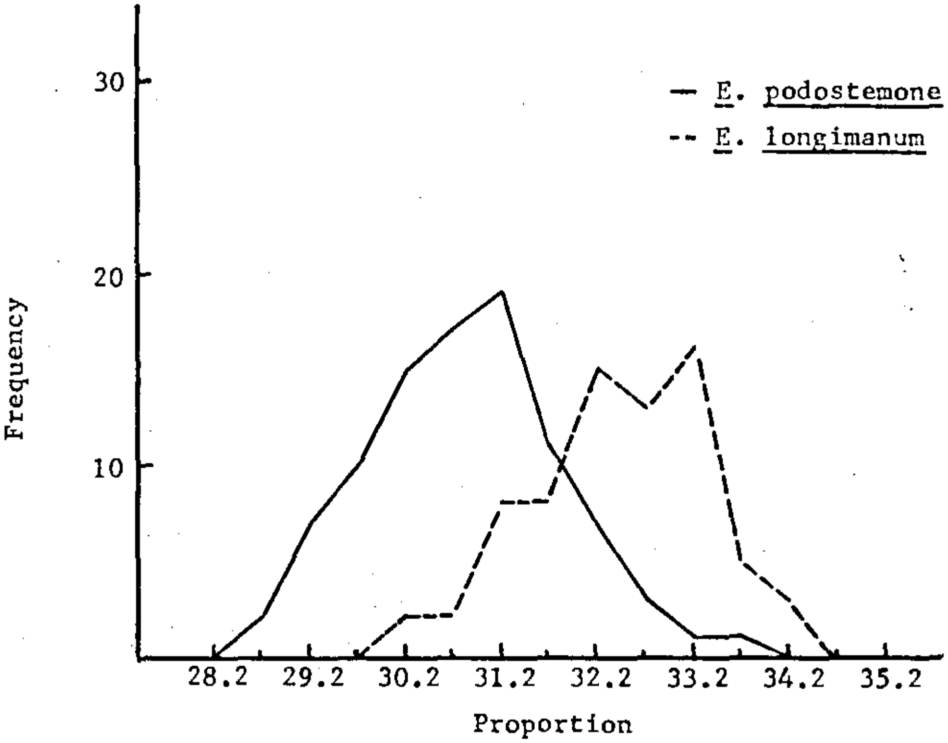


Figure 26. Predorsal length in standard length

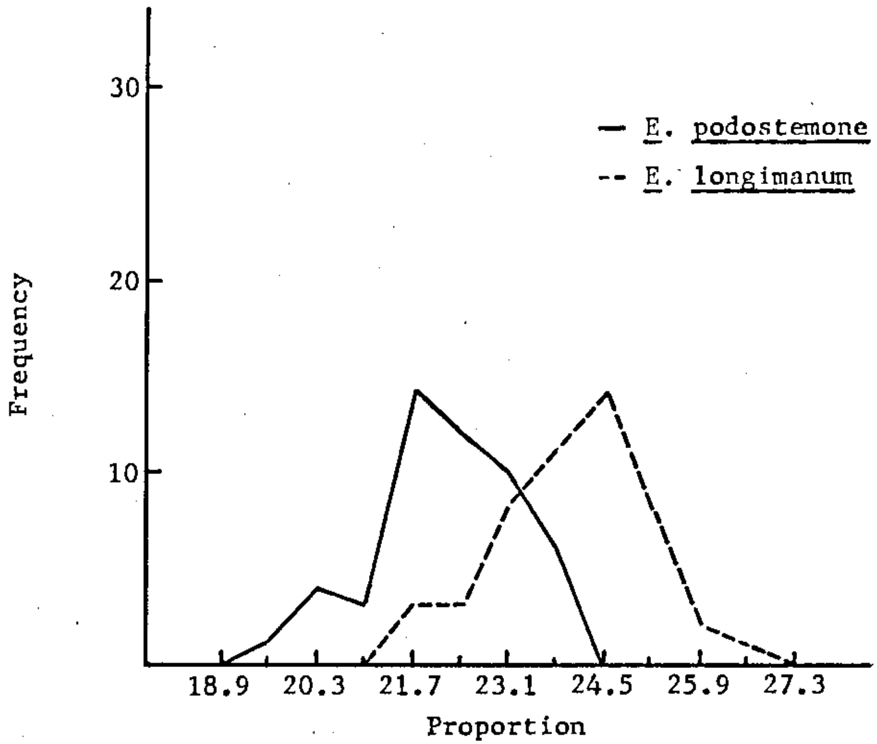


Figure 27. Snout length in head length

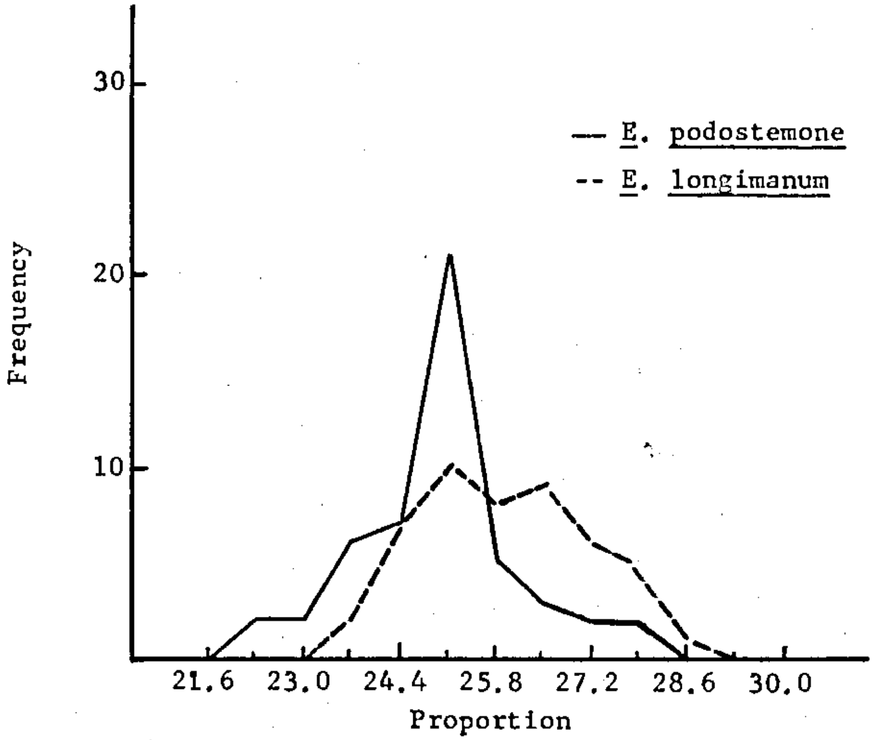


Figure 28. Length of orbit in head length

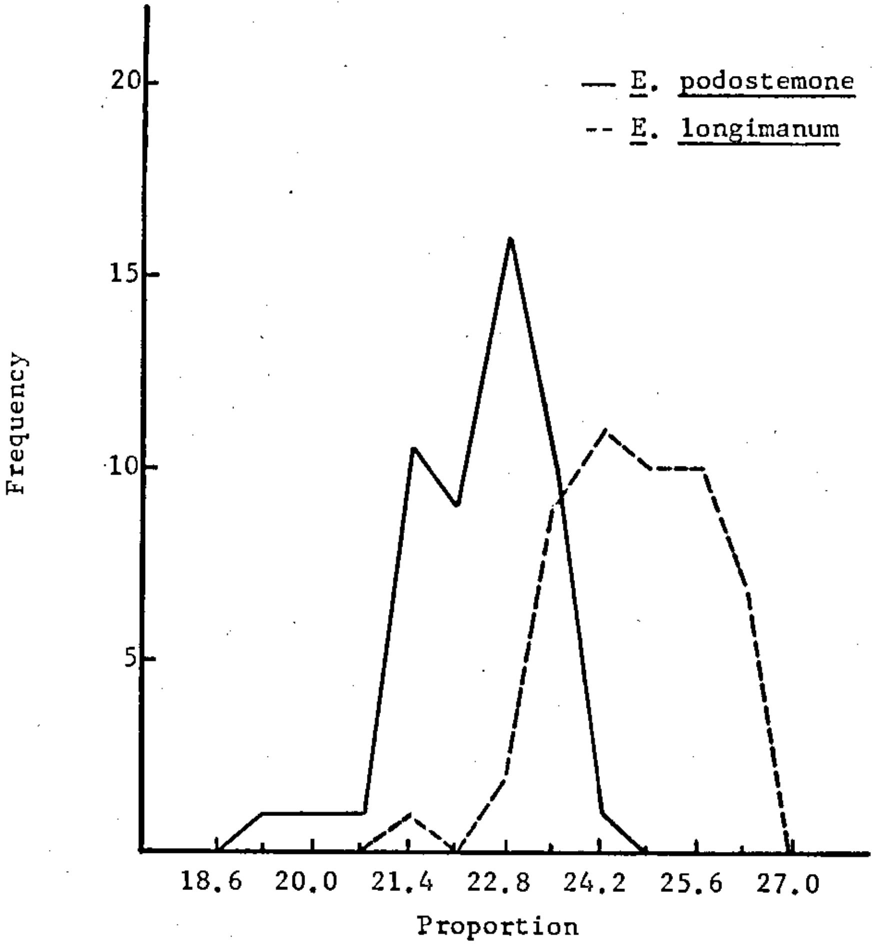


Figure 29. Lower jaw length in head length

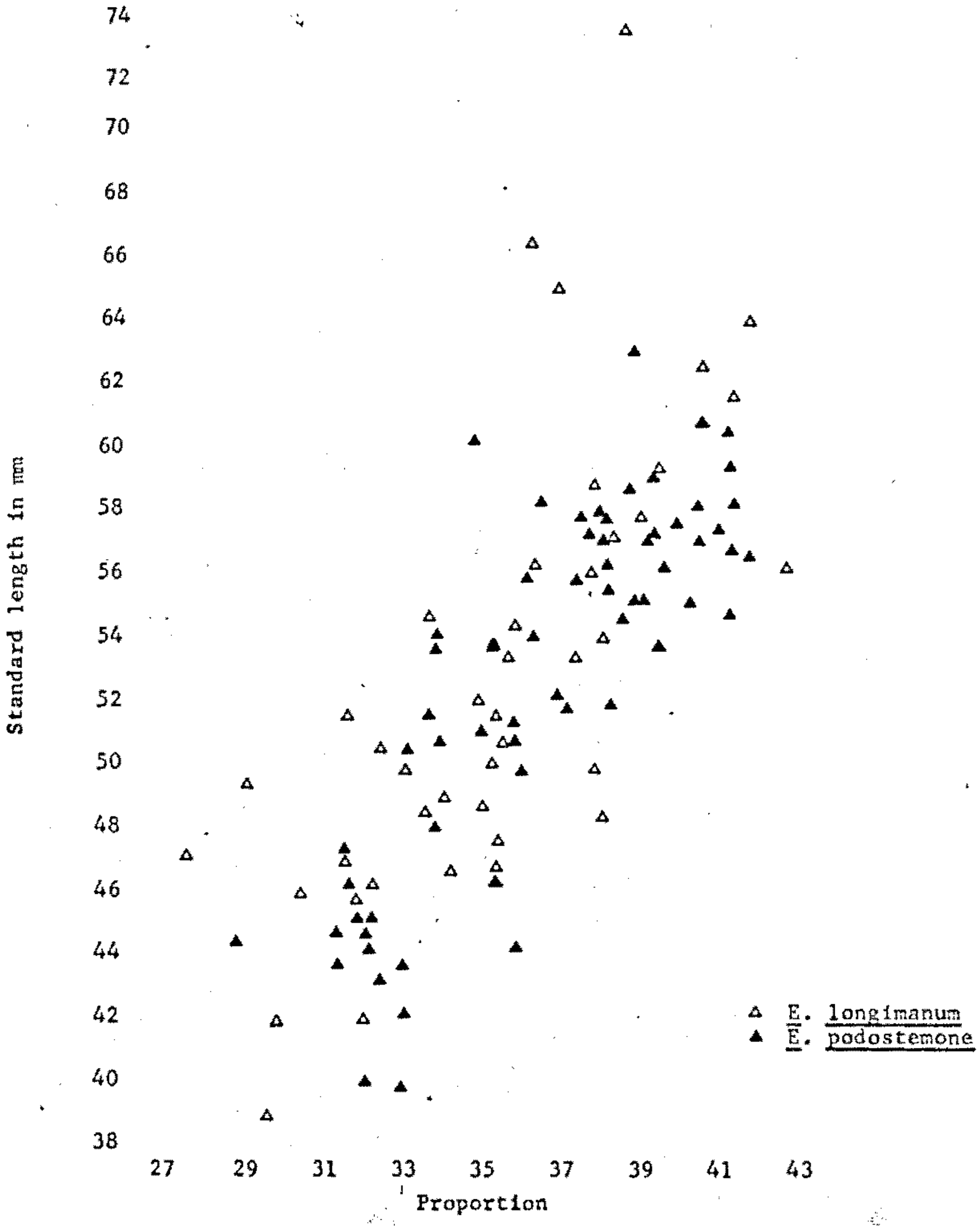


Figure 30. Scatter diagram of length of depressed second dorsal fin of males in standard length

Figure 31. Sample comparison diagrams of *E. longimanum* (A) and *E. podostemone* (B).

a. Scales in lateral line.

b. Scale rows above lateral line to origin of second dorsal fin.

c. Scale rows above lateral line to origin of first dorsal fin.

d. Scale rows below lateral line to origin of anal fin.

e. Scale rows around caudal peduncle.

f. Lateral scale rows from origin of first dorsal fin to origin or second dorsal fin.

g. Scale rows around caudal peduncle plus scales above lateral line to origin of second dorsal fin plus scales below lateral line to origin of anal fin.

Figure 31.

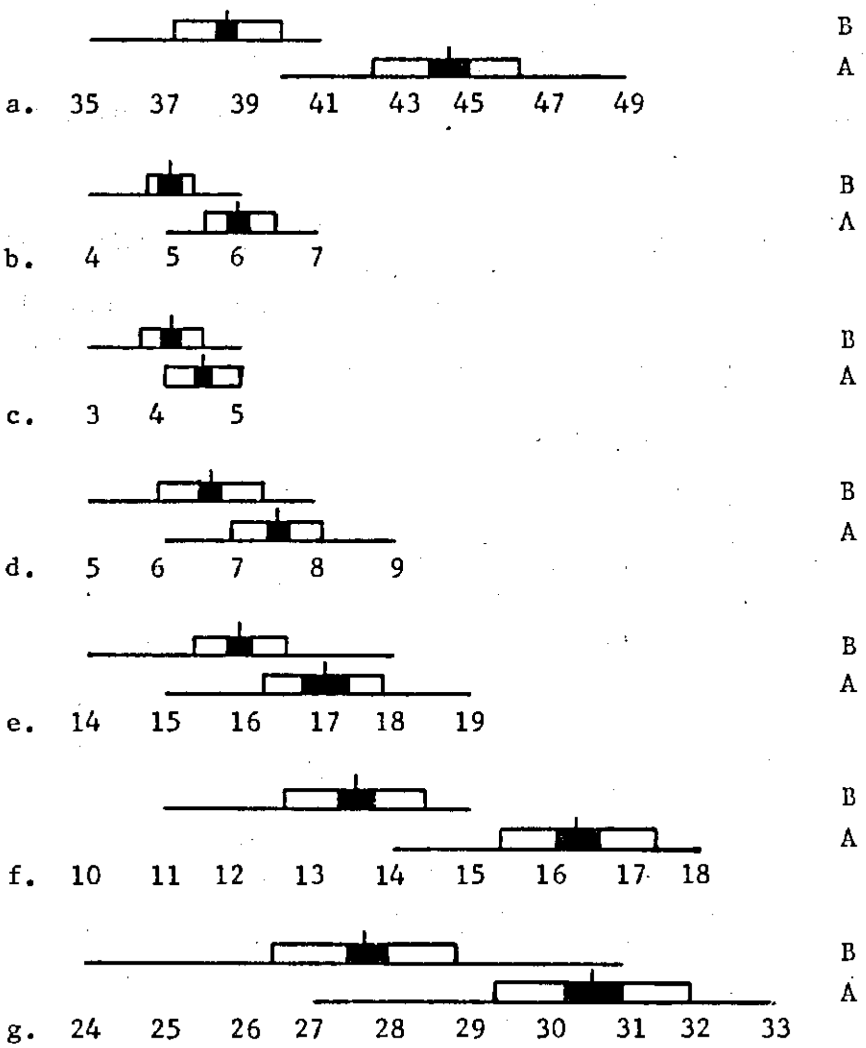

B
A
a. 35 37 39 41 43 45 47 49
B
A
b. 4 5 6 7
B
A
c. 3 4 5
B
A
d. 5 6 7 8 9
B
A
e. 14 15 16 17 18 19
B
A
f. 10 11 12 13 14 15 16 17 18
B
A
g. 24 25 26 27 28 29 30 31 32 33

Figure 32. Sample comparison diagrams of E. longimanum (A) and E. podostemone (B).

a. Spines in first dorsal fin.

b. Rays in second dorsal fin.

c. Rays in anal fin.

d. Rays in left pectoral fin.

e. Rays in right pectoral fin.

f. Pores in infraorbital canal.

g. Pores in preoperculomandibular canal.

Figure 32.

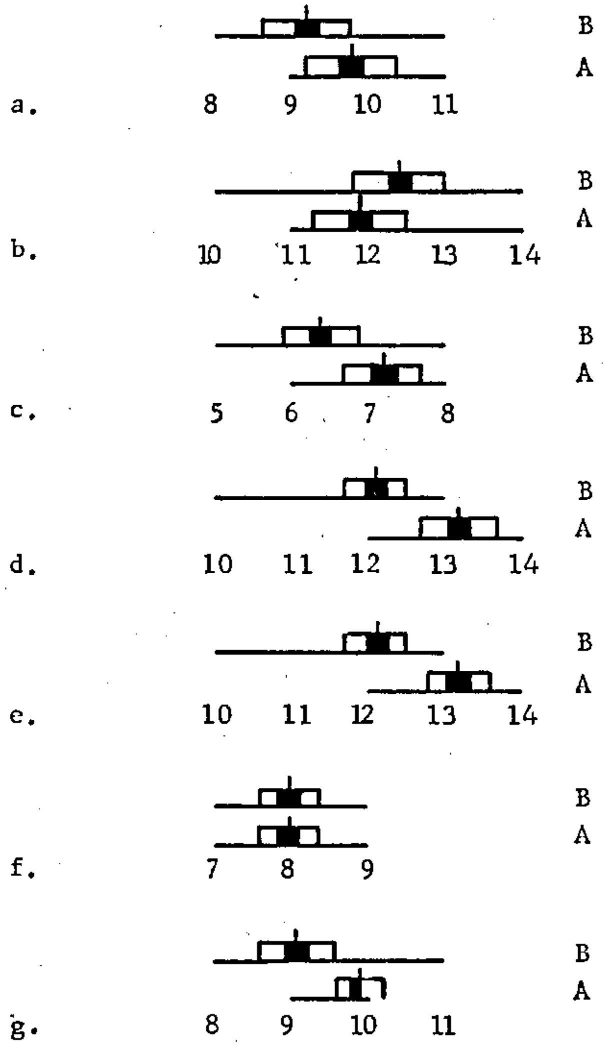

B
A
a.
8
9
10
11
B
A
b.
10
11
12
13
14
B
A
c.
5
6
7
8
B
A
d.
10
11
12
13
14
B
A
e.
10
11
12
13
14
B
A
f.
7
8
9
B
A
g.
8
9
10
11

Figure 33. Sample comparison diagrams of *E. longimanum* (A) and *E. podostemone* (B).

a. Body depth in standard length.
b. Caudal peduncle depth in standard length.
c. Head depth in standard length.
d. Head length in standard length.
e. Snout length in standard length.
f. Postorbital head length in standard length.
g. Length of longest pectoral fin ray in standard length.
h. Length of longest pelvic fin ray in standard length.

Figure 33.

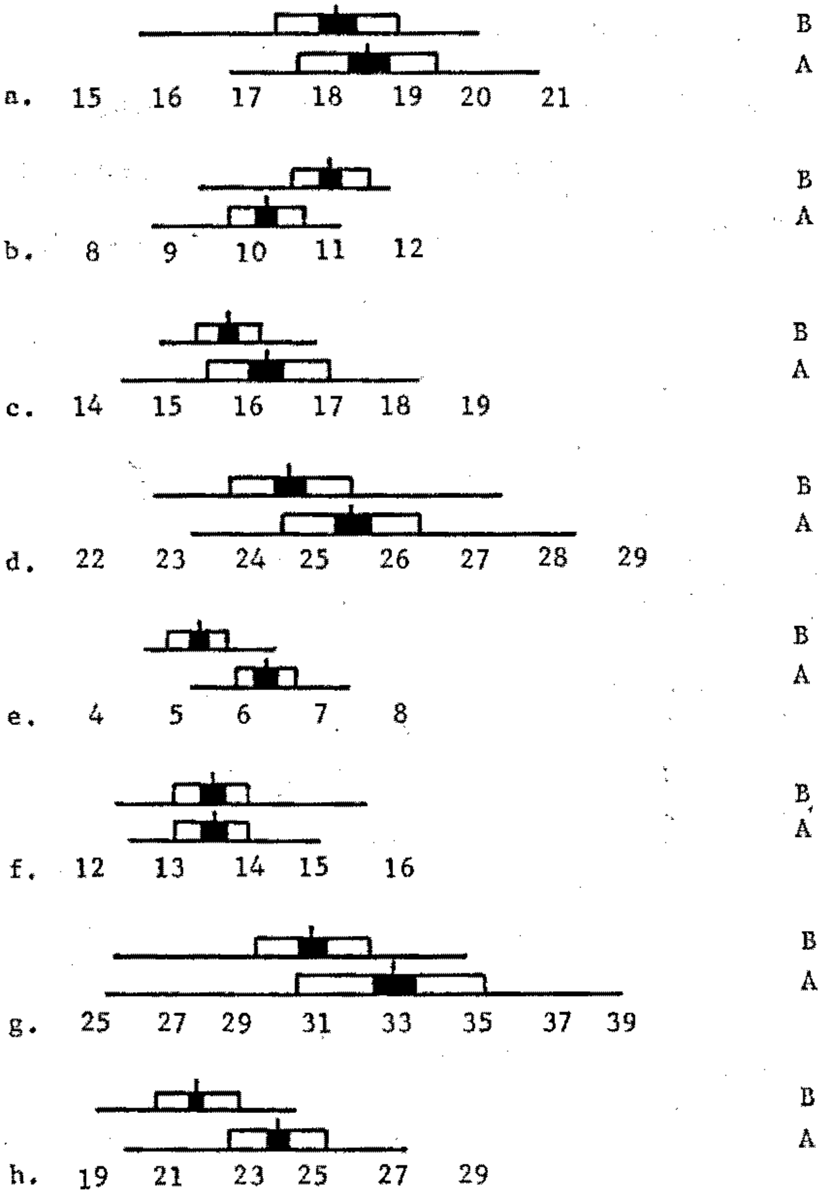

B
A
a. 15 16 17 18 19 20 21
B
A
b. 8 9 10 11 12
B
A
c. 14 15 16 17 18 19
B
A
d. 22 23 24 25 26 27 28 29
B
A
e. 4 5 6 7 8
B
A
f. 12 13 14 15 16
B
A
g. 25 27 29 31 33 35 37 39
B
A
h. 19 21 23 25 27 29

Figure 34. Sample comparison diagrams of _E_. _longimanum_ (A) and _E_. _podostemone_ (B)

a. Length of first dorsal fin base in standard length.

b. Length of depressed second dorsal fin of females in standard length.

c. Caudal peduncle length in standard length.

d. Snout length in head length.

e. Length of orbit in head length.

f. Lower jaw length in head length.

g. Predorsal length in standard length.

Figure 34.

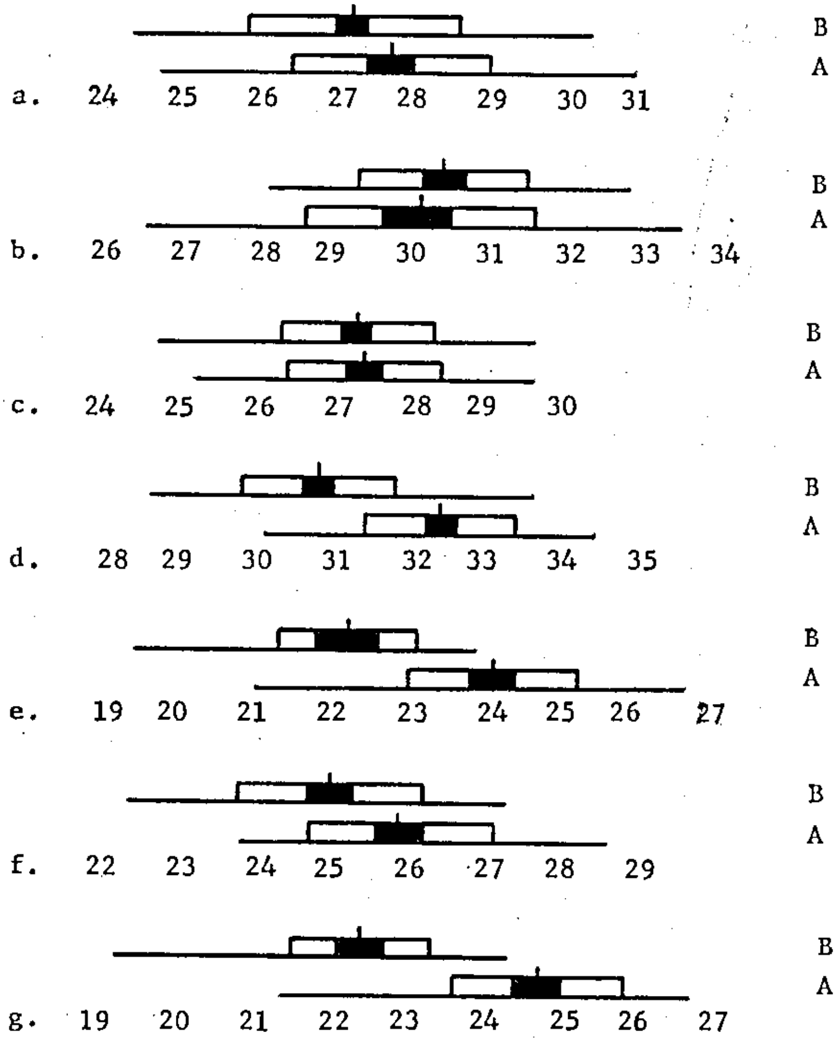
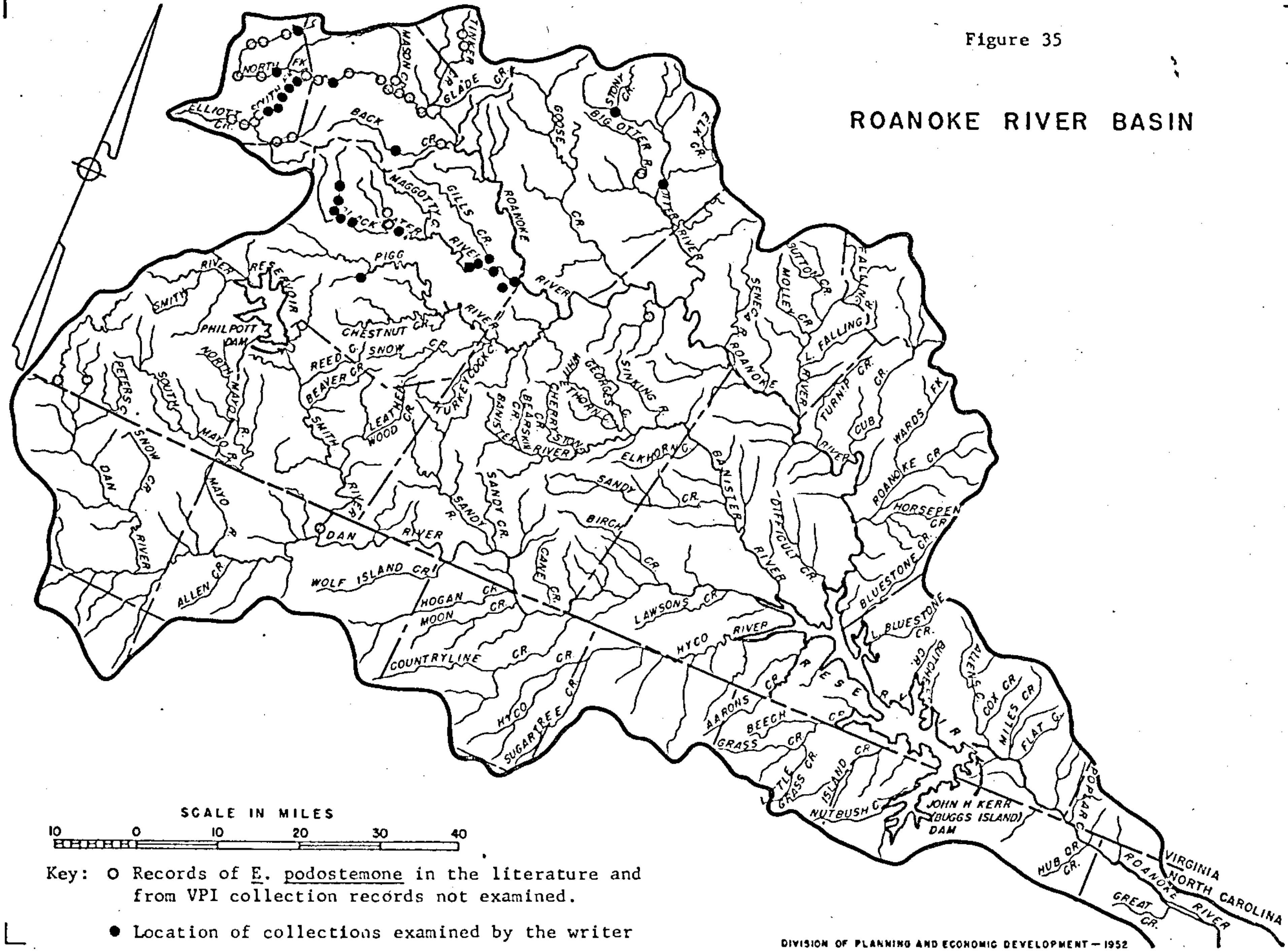

B
A
a. 24 25 26 27 28 29 30 31
B
A
b. 26 27 28 29 30 31 32 33 34
B
A
c. 24 25 26 27 28 29 30
B
A
d. 28 29 30 31 32 33 34 35
B
A
e. 19 20 21 22 23 24 25 26 27
B
A
f. 22 23 24 25 26 27 28 29
B
A
g. 19 20 21 22 23 24 25 26 27

Figure 35



Key: ○ Records of E. podostemone in the literature and from VPI collection records not examined.

● Location of collections examined by the writer

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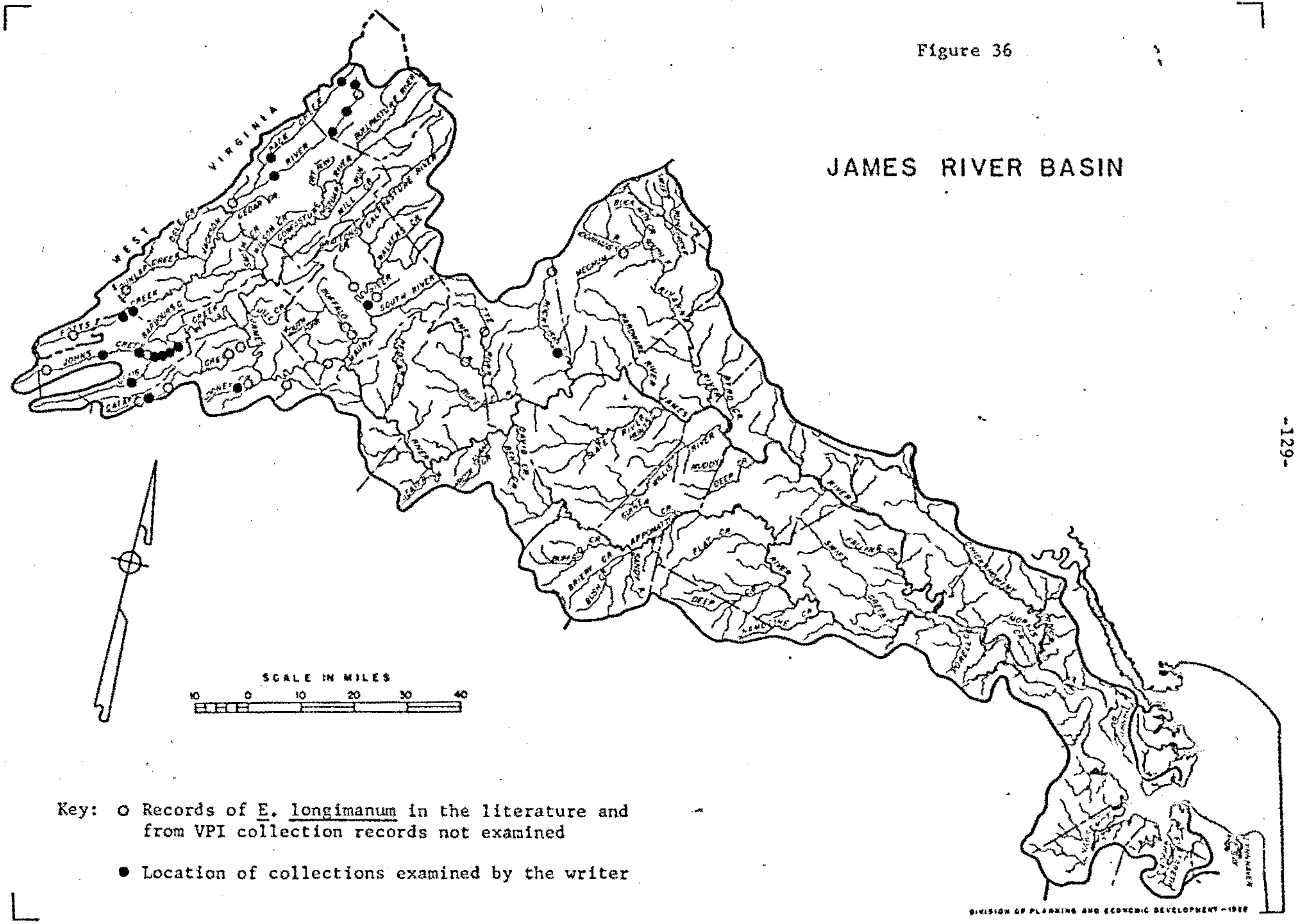
Figure 36



Key: ○ Records of E. longimanum in the literature and from VPI collection records not examined

● Location of collections examined by the writer

Abstract of Master of Science Degree Thesis

by

Robert L. Miles

A Systematic Study of *Etheostoma longimanum* and *Etheostoma podostemone* (Pisces, Percidae)

The purpose of this study was to clarify the systematic relationships between *Etheostoma longimanum*, an endemic of the James River system, and *Etheostoma podostemone*, an endemic of the Roanoke River system. Twenty-nine morphological characters were compared between the two species, using Ginsberg's criteria and sample comparison diagrams as indicators of divergence.

These two forms were shown to be separable on Ginsberg's specific or intermediate specific level in seven morphological characters. Subspecific differences were found to occur in seven other characters. These differences, as well as additional qualitative differences, are interpreted by the writer as evidence that *E. longimanum* and *E. podostemone* represent valid species. Allopatric speciation from *E. olmstedi* stock is postulated.