

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO.155

**A Revision of the
Mexican Cyprinid Fish Genus *Algansea***

by

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and

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Ann Arbor
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN

August 4, 1978

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ERRATUM

Barbour, C.D. and R.R. Miller. 1978. A Revision of the Mexican Cyprinid Fish Genus *Algansea*. Misc. Publ. Mus. Zool. Univ. Mich., 155:1-72.

After this paper went to press, we found that character 5 (PM pores, Table 7) had been erroneously coded as 1 for *A. lacustris* instead of 2. Correct coordinate-by-character loadings (Table 7) and average taxonomic distances (Table 8) are given below. OTU projections (Figs. 21 and 22) and our modified discussion (pp. 58-59) are given on the reverse side of this page. Our conclusions remain unchanged.

TABLE 7

Principal Coordinate				
I	II	III	IV	V
-	-.4	.4	-	-
.4	-	-	-	-
.5	-	-.3	-	-
-1.0	.3	-.6	-.3	-
.3	-.4	-	-	-
-	-.3	-	-	.3
.4	-	-	-	-
.3	-	.4	-	-
-	.4	-	-	-
.5	-	-	-	-
.5	-	-	-	-
-1.1	-	-	-	-
-	.4	-	-	-
-1.1	-	-	-	-
-.5	-	-1.0	.3	-
-1.1	-	-	-	-
-	.4	-	-	-
-	-.9	-	-	-
-	-.9	-	-	-
.5	-	-.3	-	-
.4	-	-.7	-	-
.5	-	-.3	-	-
.4	-	-	.4	-
-	.4	-	-	-
-1.1	-	-	-	-
-	.4	-	-	-

TABLE 8

AVERAGE TAXONOMIC DISTANCES BETWEEN THE SPECIES OF *ALGANSEA*

	<i>aphanea</i>	<i>monticola</i>	<i>barbata</i>	<i>tincella</i>	<i>lacustris</i>
<i>aphanea</i>	0.0				
<i>monticola</i>	1.241	0.0			
<i>barbata</i>	1.383	0.655	0.0		
<i>tincella</i>	1.442	0.613	0.873	0.0	
<i>lacustris</i>	1.719	1.104	1.332	0.861	0.0
<i>popoche</i>	2.352	1.725	1.877	1.427	1.471

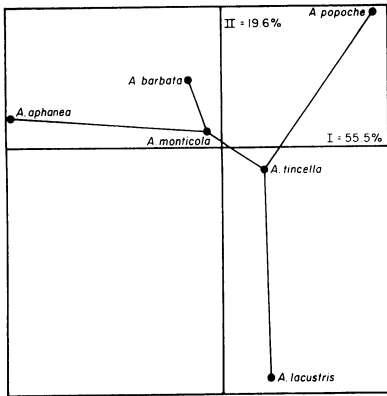


FIGURE 21

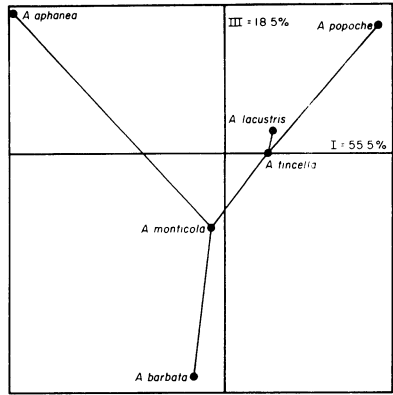


FIGURE 22

PRINCIPAL COORDINATE I. All but nine of the characters have moderate to high loadings on the first axis which accounts for 55.5% of the variation and has an eigenvalue of 9.0 (Fig. 21, Table 7)

PRINCIPAL COORDINATE II. The second axis has an eigenvalue of 3.2 and accounts for 19.6% of the variation (Fig. 21, Table 7) Finally, the moderate loading of character 1 (Length) accounts for the displacement of *A. barbata*.

PRINCIPAL COORDINATE III. The third axis has an eigenvalue of 3.0 and explains 18.5% of the variation (Fig. 22, Table 7). The high loading of character 15 (Frontal) is a major factor accounting for the displacement of *A. barbata*. Similarities between *A. lacustris*, *A. tinella* and *A. monticola* among the remaining seven characters tend to result in a central cluster of these species leaving *A. aphanea* and *A. popoche* as very similar outliers.

PRINCIPAL COORDINATES IV AND V. The fourth and fifth axes have eigenvalues of 0.6 and 0.5 respectively and account for the remaining 6.0% of the variation

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INTRODUCTION

The cyprinid fishes of the New World range southward only a short distance into Middle America, reaching their southern limit to the west and northwest of the Isthmus of Tehuantepec in southern Mexico. Along the Atlantic slope a few species extend into the tropics with one (*Dionda ipni*) ranging as far south as the Río Misantla (at 20° N lat.) in Veracruz (Hubbs and Miller, 1977). On the highlands of the Atlantic slope they occur as far south as certain tributaries of the Río Papalapan in Oaxaca (De Buen, 1955). On the Pacific side of México cyprinids reach the Río Verde basin (16° 31' N lat.) to the east of the Río Balsas drainage in Oaxaca (Cortés, 1968). As one progresses southward from the United States border on the Mexican Plateau, the number of genera and species decreases rapidly. In the large Río Lerma basin (near 20° N lat.), only three genera remain: *Algansea*, *Notropis*, and *Yuriria*. *Algansea* is found throughout the Río Lerma and contiguous areas (Figs. 1-2), with a distribution resembling that of the atherinid genus *Chirostoma* (Barbour, 1973a, b) and, to a lesser extent, that of the Goodeidae (Hubbs and Turner, 1939; Miller and Fitzsimons, 1971).

The genus *Algansea*, when described by Girard (1856), included three nominal species of *Siphateles*, which is now regarded as a subgenus of *Gila* (see Miller, 1968). The type-species, *Leuciscus tincella* Valenciennes, was designated by Jordan and Gilbert (1883). Jordan and Snyder (1900) erected the monotypic genus *Xystrosus* for a lacustrine-adapted cyprinid from Lake Chapala, Jalisco-Michoacán. *Algansea antica* Cope (syntypes, ANSP 4911-13, 16868, examined by R. R. M.), said to have come from Texas, is a synonym of *Gila bicolor* (subgenus *Siphateles*), and probably came from Nevada or an adjacent state (Fowler, 1913:69). We recognize six species within *Algansea*, of which one is described herein, including the nominal *Xystrosus popoche*. Our objectives are to clarify the systematics of *Algansea* and to discuss the evolution of the species. It is clear from this study that *Algansea* is very closely related to certain species of the genus *Gila*. As it is beyond the scope of this paper to revise that genus as well as *Algansea*, we have left any possible taxonomic changes involving the species of both groups to future workers.

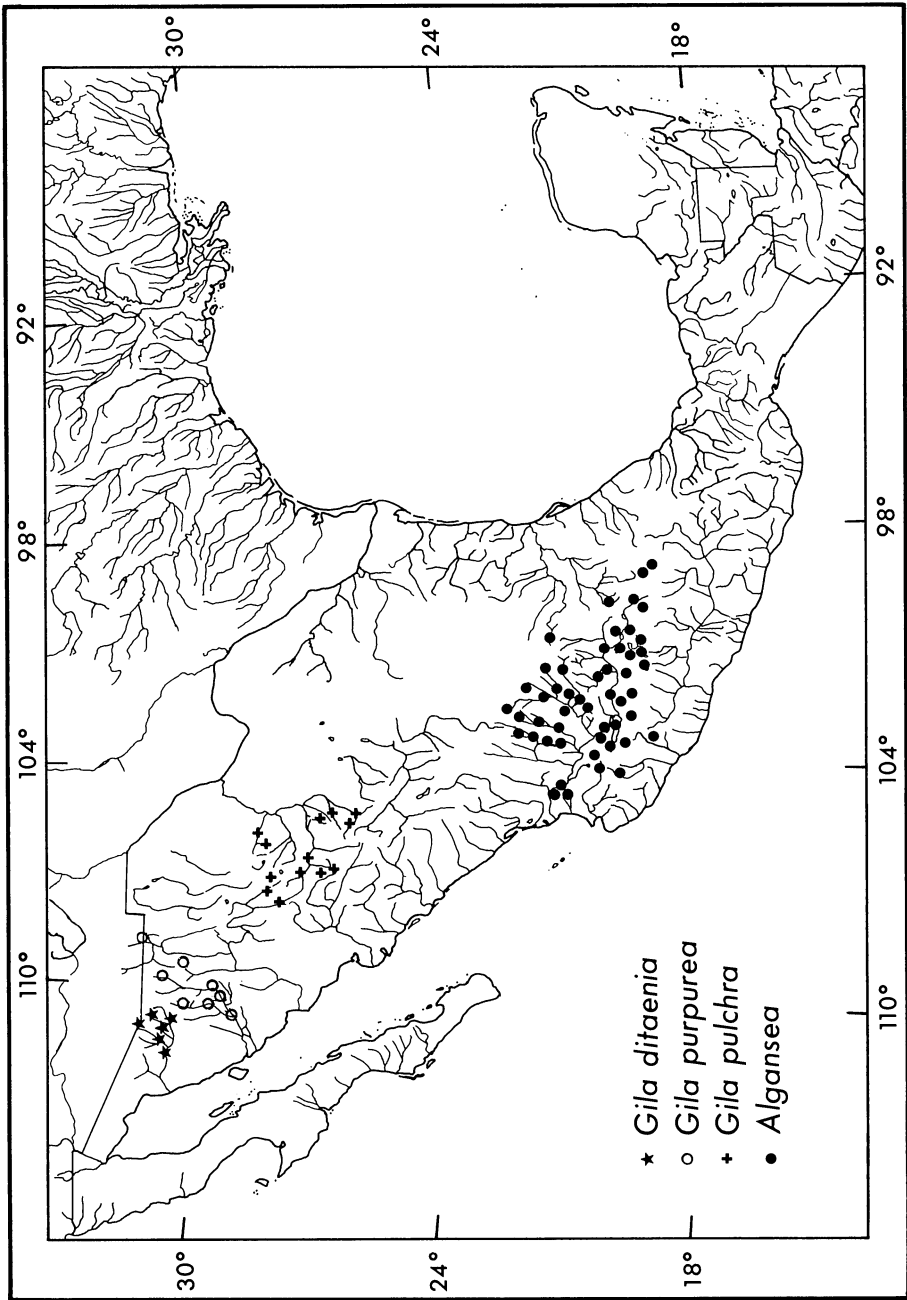


Fig. 1. Distribution of the genus *Algansea* and of three species of the subgenus *Temeculina* of the genus *Gila*.

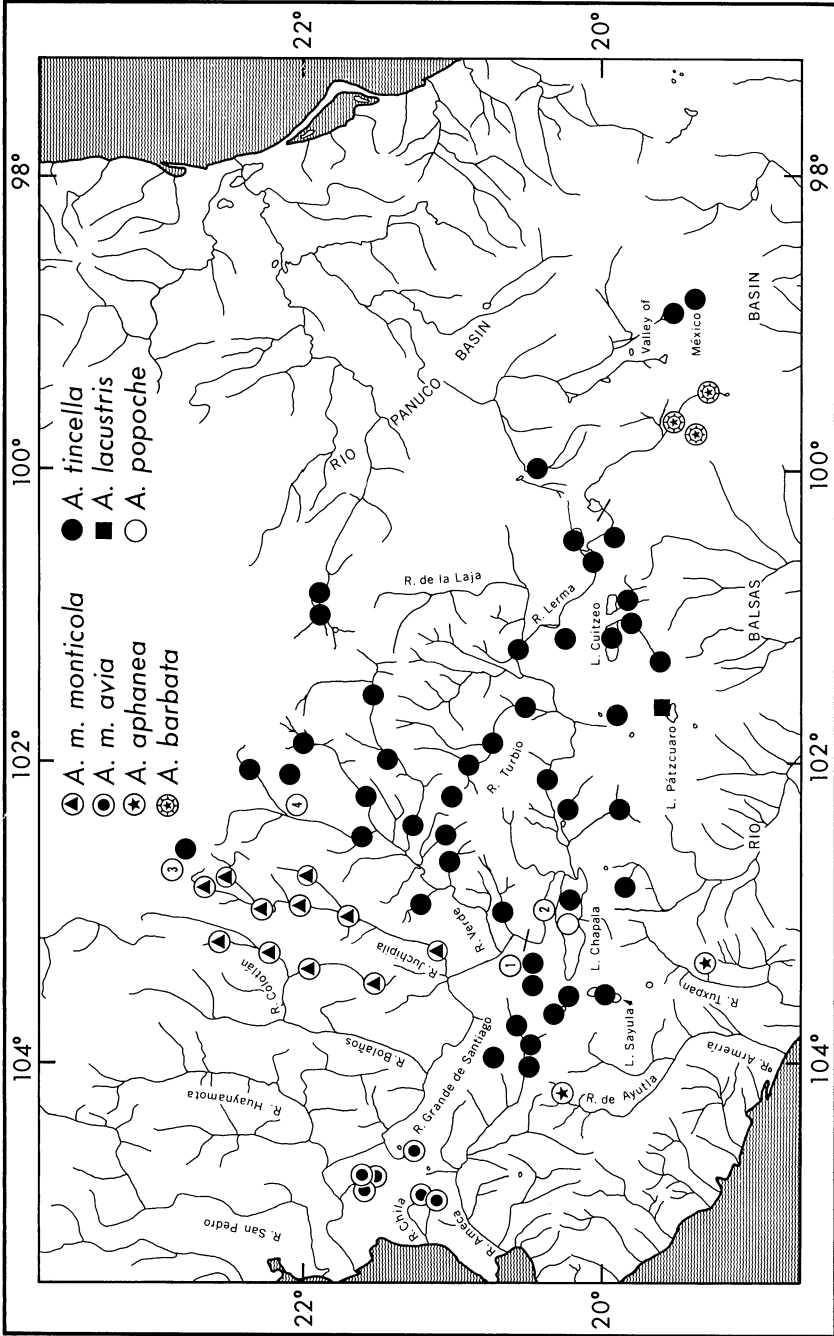


Fig. 2. Distribution of the species of *Algansea*. Not all collections at a given locality or within a lake are shown. Lake Chapala species also occur in adjacent parts of Río Lerma and Río Grande de Santiago. The circled numbers represent the following cities: (1) Guadaluajara, (2) Poncitlán, (3) Zacatecas, (4) Aguascalientes; the solid bars across Río Lerma-Santiago indicate, from west to east, the waterfalls at Juanacatlán and below Tepuxtepec dam. Abbreviations: L., Lake; R., Río.

MATERIALS AND METHODS

The majority of the specimens examined for this study were collected by us and are housed in the Museum of Zoology, University of Michigan (UMMZ). Specimens needed to fill in distributional gaps or increase the representation of a species were borrowed from the institutions given below.

All counts and measurements (expressed as a percentage of the standard length) were made according to the methods described by Hubbs and Lagler (1958). All body lengths given are standard length. The procedure for counting the pores of the cephalic lateral-line system followed Illick (1956). Counts of the paired canals were made on both the left and the right side of the head. Mean values were calculated and tested for significance of difference at the .05 level by means of Student's t-test (Simpson, Roe, and Lewontin, 1960). Where no significant difference was found, counts are given for the left side only. Counts for *A. barbata* are given for both sides because the small sample size precluded statistical analysis.

Osteological observations were made on specimens cleared and stained according to the method of Taylor (1967) (Figs. 9, 11, 13C, 14A-C, 15C, 16A-B, 17) and on skeletons cleaned with the aid of dermestid beetles (Figs. 10, 12, 13A-B, 14B, 15A-B, 16C). Supraorbital bones (of no taxonomic value) were omitted from all drawings of neurocrania and the pore openings of the infraorbital canal were excluded from the drawings of the infraorbital series. Though our investigations revealed some interesting differences between the species, they should not be considered definitive as the skulls were not completely disarticulated and the range of variation within populations (other than those of *A. tincella*) was not determined. Vertebral counts, including the first four fused vertebrae and counting the urostyle as one, were made from radiographs. Measurements of the pharyngeal arch followed the methods of Uyeno (1961, Pl. 26). Osteological terminology follows that of Harrington (1955), Ramaswami (1955a, b), and Weitzman (1962).

The following abbreviations appear in this paper: hwy (highway), km (kilometers), mm (millimeters), trib. (tributary), jct. (junction). Geographic directions are indicated by the initial letters of the cardinal points of the compass, North, South, East, West, or various combinations thereof. Osteological abbreviations are as follows:

ART—Articular; ASP—Ascending process of maxilla; BOC—Basioccipital; DE—Dentary; DSPH—Dermosphenotic; EOC—Exoccipital; EPO—Epiotic; FR—Frontal; LE—Lateral ethmoid; LOF—Lateral occipital foramen; PA—Parietal; PAP—Palatine process; PE—Preethmoid; PMP—Premaxillary process of maxilla; PPBO—Pharyngeal process of basioccipital; PTF—Posttemporal fossa; PTO—Pterotic; RA—Retroarticular; ROP—Rostral process of maxilla; RS—Recessus sacculus; SE—Supraethmoid; SOC—Supraoccipital; SPH—Sphenotic.

Osteological material (all in UMMZ unless otherwise noted) other than that of *Algansea* was examined as follows:

Agosia chrysoaster, 162669 (1); *Clinostomus elongatus*, OSUM 11088 (1); *C. funduloides*, OSUM 21060 (1); *Dionda dichroma*, 189573 (3); *Gila alvordensis*, 186517 (1); *G. atraria*, 174542 (1); *G. bicolor*, 177085 (1), 174438 (1); *G. copei*, 173789 (1); *G. coerulea*, 176740 (1); *G. crassicauda*, 87277 (1); *G. cypha*, 179577 (1); *G. ditaenia*, 141945 (1); *G. orcutti*, 132141 (1); *G. pandora*, 177322 (1); *G. pulchra*, 61731 (1); *G. purpurea*, 157249 (1); 157257 (1), 184894 (1); *G. robusta*, 178691 (1); *Hesperoleucus symmetricus*, 179599 (1); *Lavinia exilicauda*, 178871 (1); *Lepidomeda albivallis*, 181747 (1); *L. vittata*, 179572 (1); *Moapa coriaca*, 177086 (1); *Mylocheilus caurinus*, 177107 (1); *Mylopharodon conocephalus*, 179598 (1); *Nocomis raneyi*, 173092 (1); *Notropis atherinoides*, 172435 (1); *N. aztecus*, 172173 (2), 189622 (1), 192373 (4); *N. boucardi*, 178579 (3); *N. calientis*, 192395 (2); *N. chalybaeus*, 198733 (1); *N. cornutus*, 172437 (1); *N. galacturus*, 198726 (1); *N. heterolepis*, 198731 (1); *N. hudsonius*, 170991 (1); *N. imelda*, 188855 (2); *N. lutrensis*, 113359 (1); *N. nazas*, 161725 (2); *N. sallei*, 182346 (3); *Notropis* sp. (from México), 172218 (3); *Orthodon microlepidotus*, 179936 (1); *Plagopterus argentissimus*, 177099 (1); *Pogonichthys macrolepidotus*, 94143 (1), 178870 (1); *Ptychocheilus grandis*, 181929 (1); *P. oregonensis*, 177106 (1); *Relictus solitarius*, 124786 (1), 177095 (1); *Rhinichthys cataractae*, 179563 (1); *Richardsonius balteatus*, 177324 (2); *Semotilus atromaculatus*, 189364 (1); *Yuriria alta*, 179703 (1), 192203 (3), 192267 (3).

The Spanish words "lago" and "laguna" have been translated as "lake." The word "río," river, has been left in Spanish to avoid the sort of awkwardness and ambiguity which so often accompanies literal translations (e.g., Río San Juan del Río, San Juan del Río River; Río Grande de Morelia, Great River of Morelia or, worse, Grande de Morelia River).

DIAGNOSTIC AND DESCRIPTIVE CHARACTERS

There are few characters which, by themselves, will diagnose individual species of *Algansea*. The following brief outline lists those that proved most useful for separating species and species groups as well as illustrating presumed phylogenetic relationships and morphological trends within the genus.

OSTEOLOGY.—The following bones showed varying degrees of interspecific variation: dentary, maxilla, quadrate, and urohyal. The configuration of the bones of the otic and occipital region, the supraethmoid, and the infraorbital series also revealed differences among species, as did the shape of the pharyngeal arch and the relative strength of the teeth. No useful differences were found in the axial or appendicular skeleton.

MERISTIC CHARACTERS.—The number of dorsal fin rays helps to distinguish *A. monticola monticola* from *A. m. avia*. The total number of gill rakers in the external row of the first gill arch is diagnostic for *A. popoche*. The latter count and the number of preoperculo-mandibular pores are useful for separating species groups, whereas the number of median lateral scales revealed interesting infraspecific variation in *A. monticola avia* and *A. tincella*.

MORPHOMETRIC CHARACTERS.—Considerable infraspecific variation, particularly within *A. tincella* and *A. monticola avia*, diminished the usefulness of body proportions as taxonomic characters. No trends or patterns were uncovered which might elucidate phylogenetic pathways. The following measurements were useful in distinguishing between

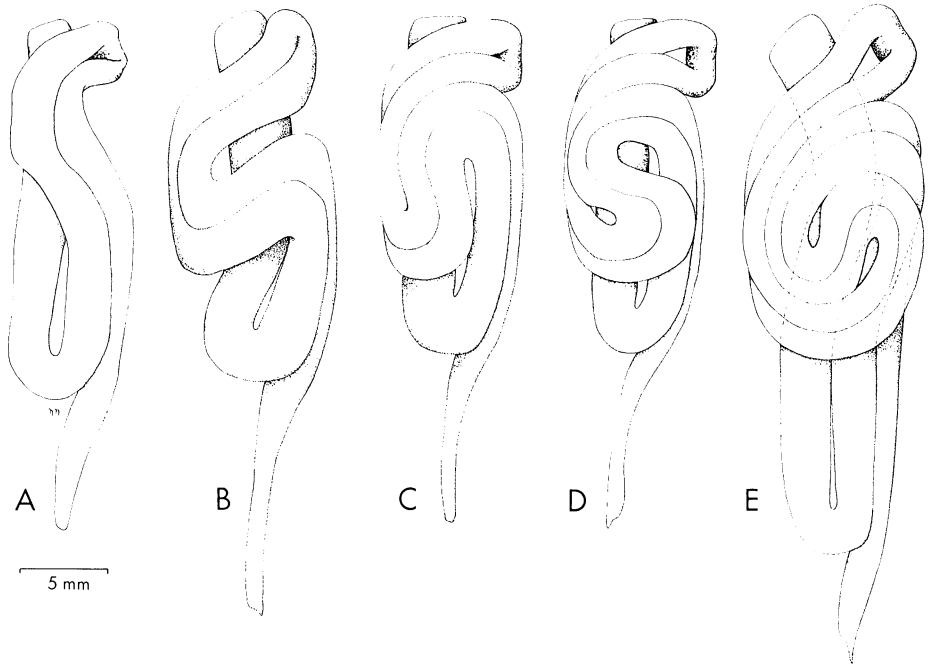


Fig. 3. Variation of gut coiling in *Algansea*: (A) *A. monticola avia*, UMMZ 172238, from a specimen 78.1 mm; (B) *A. barbata*, P 966, 103.2 mm; (C-D) *A. tincella*, UMMZ 172220, 68.2 and 84.9 mm; (E) *A. popoche*, UMMZ 167717, 138.4 mm.

certain species: interorbital width, distances from the snout to the origins of the anal and pelvic fins, and the lengths of the mandible, head, and postorbital part of the head. Sexual dimorphism was most noteworthy in the lengths of the pectoral and pelvic fins.

MORPHOLOGY OF THE HEAD.—There is considerable variation in the shape of the head and the relationship of its component structures within *Algansea*. Differences between species and species groups may be seen in the position of the mouth relative to the snout, the position of the eyes and the inferred field of vision, the presence or absence of barbels, and the fleshiness of the lips.

VISCERAL ANATOMY.—The configuration of the gut (Fig. 3) shows an increasing complexity of coiling from the small to the large species of *Algansea*. This character is most useful in distinguishing between groups of species.

PIGMENTATION.—The details of pigmentation tend to be variable in *Algansea*, particularly in the wide-ranging species *A. tincella*. The interpretation of this characteristic is further complicated by the fact that some of the species live in turbid water and always present a “washed out” appearance (e.g., see Fig. 7). However, the presence of melanophores on or between the median caudal rays, the distinctness of the black spot at the base of the caudal fin, and the degree to which the

dark lateral stripe, when present, is set off from the dark dorsum, are all useful taxonomic characters.

NUPTIAL TUBERCULATION.—The size and distribution of the nuptial tubercles of *Algansea* tend to resemble those of *Gila*. Although their distribution appears to vary somewhat between species, our interpretation of this character has been hampered by insufficient numbers of specimens collected during the spawning period.

SCALE RADII.—The distribution of radii on the scales is a useful group character in North American cyprinids (Jenkins and Lachner, 1971). Within *Algansea*, all species except two have radii on all scale fields. In *A. popoche* and *A. lacustris*, the radii on the anterior field are obsolete or lacking.

REPRODUCTIVE BIOLOGY.—Even though it has not been possible for us to make monthly collections of any of the species of *Algansea*, it is apparent from the literature and our own observations of gonads that some of the species spawn at different times of the year. Estimates of temporal reproductive isolation have been of primary importance in determining the taxonomic status of a species pair that is not morphometrically distinct: *A. tincella* and *A. lacustris*.

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The following individuals materially aided this study through the loan of specimens in their care: J. Alvarez del Villar, Instituto Politecnico Nacional, México, D.F. (P); S. Contreras-Balderas, Universidad Autónoma de Nuevo León, Monterrey (SCB); E. A. Lachner and W. R. Taylor, U.S. National Museum of Natural History (USNM); R. D. Suttkus and R. C. Cashner, Tulane University (TU); and L. P. Woods, Field Museum of Natural History (FMNH). We thank G. S. Myers and W. Freihofer, California Academy of Sciences (CAS-SU), James E. Böhlke, Academy of Natural Sciences of Philadelphia (ANSP), and P. H. Greenwood, British Museum of Natural History (BMNH), for permission to examine types in their care. We are also grateful to M. L. Bauchot, Museum National d'Histoire Naturelle, Paris, for examining the type-species of *Algansea*, *Leuciscus tincella*, for us. T. M. Cavender, Ohio State University Museum of Zoology (OSUM), kindly allowed us to examine specimens in his care. Gerald R. Smith generously read and much improved the manuscript, as did two anonymous reviewers. Frances H. Miller typed and proofread rough drafts.

The drawings in Fig. 3 were executed by Nancy A. Neff. All others except those in Figs. 1 and 2 are the work of Carole W. Christman, former Staff Artist of the Museum of Zoology. The photographs are by Louis P. Martonyi. Their efforts considerably enhance our presentation.

We also express our sincere appreciation to Richard J. Jensen, Wright State University, for statistical aid and for leading one of us (C. D. B.)

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GENUS *ALGANSEA* GIRARD

Algansea Girard, 1856:182 (original description, including 3 nominal species of *Siphateles*, a subgenus of *Gila*). Jordan and Gilbert, 1883: 245 (type-species designated as *Leuciscus tincella* Valenciennes). Jordan and Evermann, 1896:211 (description and relationships of three species, including one not now assigned to *Algansea*). Regan, 1906-08:143, 151 (characters, relationships, key to species). Eigenmann, 1909:303-304 (distribution, list of species). De Buen 1946a: 267 (key to species); 1946b:109 (list of species). Alvarez, 1950:47 and 1970:55, 58 (keys to genus and species).

Xystrosus Jordan and Snyder, 1900:123, fig. 5 (original description, type-species, *X. popoche*). Meek, 1904:43, fig. 7 (description, range, food value, spawning season). Alvarez, 1950:47, 1970:54, 56 (key, description, size, range).

RANGE.—Widespread on the Mesa Central of México in the Río Lerma and contiguous interior basins including the Valley of México in the east, Lake Pátzcuaro and the Río Grande de Morelia-Lake Cuitzeo basin in the transverse volcanic axis to the south, and lakes Magdalena, Atotonilco, and Sayula in the west. Occurs also on the Atlantic slope in the Río San Juan del Río, Querétaro, and the Río Santa María, San Luis Potosí, headwaters of the Río Pánuco. On the Pacific slope (exclusive of the Lerma basin), *Algansea* is present in a tributary to the Río Balsas south of Tocumbo, Michoacán, in a tributary to the Río Tuxpan in the Coahuayana basin, in the Río Ayutla, a headwater of the Río Armeria, in the Río Chila near Compostela, Nayarit, and in the headwaters of the Río Ameca near Ameca, Jalisco. To the north, the genus occurs in the ríos Verde, Juchipila, and Colotlán, the first three northern tributaries of the Río Grande de Santiago, and in tributaries to the lower portion of this river which drain the northwest corner of the Mesa Central between Santa María and Tepic, Nayarit (Fig. 2).

DIAGNOSIS.—Rather elongate cyprinid fishes of medium to moderately large size (90 to about 230 mm maximum SL) and uniform depth;

snout usually blunt, mouth subterminal to strongly oblique; pharyngeal teeth 0,4-4,0, their tips slightly hooked or not, with a moderate to well-developed grinding surface (obsolete or lacking on the first tooth in *A. monticola monticola*, *A. m. avia*, and *A. aphaea*); dermosphenotic plate-like, wider than long (tubular in *A. aphaea*, Fig. 17A); radii present on all scale fields except in *A. popoche* and *A. lacustris* in which those on the anterior field are obsolete or lacking; a small maxillary barbel may be present (often hard to detect); breeding individuals without noteworthy nuptial coloration; nuptial tubercles of males and females small to minute, usually aligned along the entire dorsal length of pectoral rays 3 to 6, restricted to distal two-thirds of ray 2 and to more median portions of rays 7 to 10 or 11 (apparently restricted to median portions of pectoral rays 2-10 in *A. m. monticola*); tubercles present on top and probably side of head, as in *A. tincella* where they extend to about level of lower margin of eye, but may also be present on dorsal surface of body and on rays of dorsal, anal, and pelvic fins; scales moderately small to very small, the modal number in the lateral line ranging from 55 to 85, the mean for the genus usually greater than 60; dorsal and anal fins small, each with 7 or 8 rays (usually D 8, A 7), the dorsal origin lying over the pelvic insertion; pectoral rays 13 to 19; pelvic rays usually 8 or 9, frequently 10 in *A. popoche*; gill rakers 5 to 25, except in adults of *A. popoche* which have 53 to 87; total vertebrae 33 to 42; peritoneum usually dark brown or black; intestinal coiling varying from a simple loop to a counter-clockwise directed, double flexure with the apex directed anteriorly; pigmentation variable, living individuals usually bicolored, dark brown or gray above, creamy white or silvery below; dark brown or black median lateral stripe typically developed from head to caudal base and set off dorsally by a parallel light-colored band; discrete spot usually at midbase of caudal fin, occasionally present as an intensification or widening of median lateral stripe. Its closest relationships lie with certain members of the genus *Gila* (see PHYLOGENY OF *ALGANSEA*).

KEY TO THE SPECIES AND SUBSPECIES OF *ALGANSEA*

- | | | |
|----|--|---|
| 1a | Maxillary barbel present | 2 |
| 1b | Maxillary barbel absent | 5 |
| 2a | Mouth terminal | 3 |
| 2b | Mouth subterminal, overhung by snout | 4 |
| 3a | Dorsal rays usually 7; spot at base of caudal fin not extending onto median caudal rays or interradial membranes; gut may be coiled as in Fig. 3A or B | <i>A. monticola monticola</i> (Fig. 5A) |
| 3b | Dorsal rays usually 8; spot at base of caudal fin may extend onto median caudal interradial membranes only; gut coiled as in Fig. 3A | <i>A. monticola avia</i> n. subsp. (Fig. 4) |
| 4a | Gut coiled as in Fig. 3B | <i>A. barbata</i> (Fig. 5B) |
| 4b | Gut coiled as in Fig. 3A | <i>A. aphaea</i> n. sp. (Fig. 6) |

- 5a Total number of gill rakers on first arch 9-25; gut coiled as in Figs. 3C, D 6
- 5b Total number of gill rakers on first arch 49-84 (48-82 mm SL: 49-70;
greater than 84 mm SL: 64-84; see Fig. 20) *A. popoche* (Fig. 8B)
- 6a Scales with well-developed radii on lateral and posterior fields only;
faint remnants of secondary radii may be present on anterior field;
median lateral scales 79-90 (modal number about 85) *A. lacustris* (Fig. 8A)
- 6b Scales with well-developed radii on all fields; median lateral scales 52-85
(modal number between 65 and 70) *A. tincella* (Fig 7)

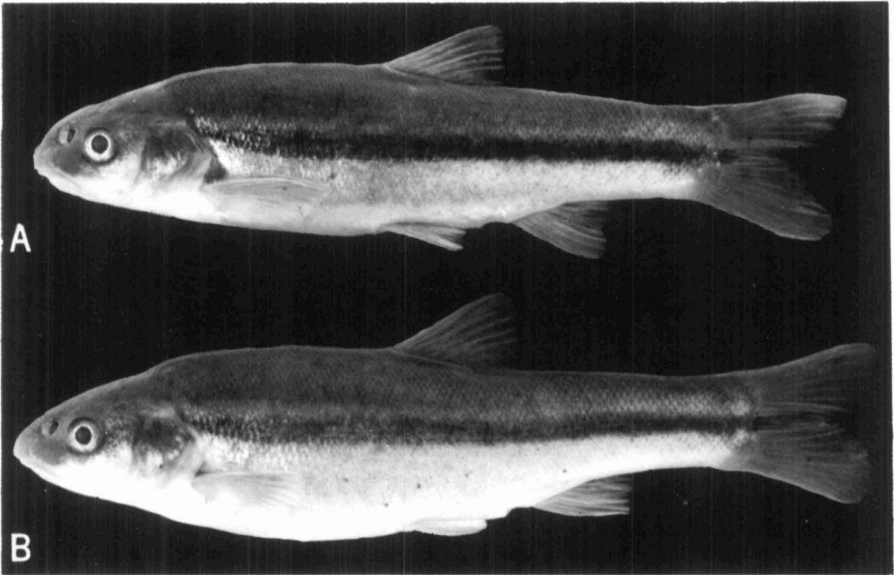


Fig. 4. *Algansea monticola avia*: (A) male, 67.9 mm, UMMZ 172238; (B) holotype, female, 73.4 mm, UMMZ 193378.

SPECIES ACCOUNTS

Algansea monticola avia, new subspecies

Fig. 4

RANGE.—Interior waters, tributaries of the Río Grande de Santiago, and headwaters of the Río Chila, at elevations between about 760 and 975 meters, that drain the margins of the northwestern corner of the Mesa Central, from near Santa María del Oro on the east to Tepic and thence southward to just beyond Compostela—all in Nayarit (Fig. 2).

DIAGNOSIS.—Barbels present; gill rakers 5 to 10; gut in the form of a simple loop (Fig. 3A; Group 2 of Kafuku, 1958); black spot at base of caudal fin represented by widening of the median lateral stripe or intensification of pigmentation, which, when present on caudal fin, occurs on median interradiial membranes only; dark lateral stripe set off from dark dorsum by light band less than width of pupil; scattered melanophores ventral to lateral stripe usually do not extend to pelvic

fins; dorsal rays 7 (5 specimens), 8 (196), 9 (7); mouth terminal, upper lip not overhung by snout.

TYPES.—Holotype, UMMZ 193378, an adult female 73.4 mm from a tributary to the Río Grande de Santiago about 4.8 km NE of hwy 15 on road to Santa María del Oro (42 km SE Tepic), Nayarit, 27 March 1955, R. R. Miller and J. T. Greenbank. Taken with the holotype were 141 paratopotypes, UMMZ 172238 (15-95 mm, 2 cleared and stained). Additional paratypes, all from the State of Nayarit, are: UMMZ 172042 (95, 16-77 mm) and TU 30817 (13), Arroyo de Mazatán (trib. Río Chila) at Mazatán, 11.3 airline km SSW Compostela, 17 February 1955; UMMZ 172047 (45, 23-80 mm, 4 cleared and stained), arroyo about 7.2 km NE Tepic on road to Puga, 18 February 1955; UMMZ 172050 (107, 17-79 mm), 18 February 1955, and UMMZ 192188 (129, 15-87 mm, 4 cleared and stained), trib. Río Chila about 27.4 km S Tepic on hwy to Compostela (9.2 km N Compostela), 17 April 1969; UMMZ 172112 (136, 28-74 mm, 6 cleared and stained) and TU 30818 (15), Río Compostela just S Compostela, 25 February 1955; UMMZ 172241 (7, 38-61 mm, 1 cleared and stained), Manantial El Sacristán, 1.3 km NW plaza of Tepic, 28 March 1955; UMMZ 178311 (471, 18-59 mm, 5 cleared and stained) and TU 30816 (20), stream at hwy 15 crossing, 27.4 km SE Tepic, 24 February 1957; UMMZ 184841 (15, 23-41 mm), Rancho de Tamarindo, 7.2 km E Tepic and about 1.6 km S hwy 15, 19 March 1959; UMMZ 192167 (1, 63 mm), at San Cayetano bridge on hwy 15, 4.8 km W of road jct. to Pantanal, 19 April 1969.

DESCRIPTION.—Holotype with 73 median lateral scales and 7 gill rakers on the first arch. Frequency distributions for these characters and the total number of preoperculo-mandibular pores are given in Tables 1-3. Other counts based on pooled data from throughout the species range follow; those including the holotype are italicized. Predorsal scales: 30(1), 31(3), 32(10), 33(13), 34(19), 35(22), 36(26), 37(19), 38(26), 39(24), 40(14), 41(12), 42(9), 43(12), 44(8), 45(4), 46(1), 47(3), 48(1), 49(3); scale rows between origin of dorsal fin and lateral line: 10(4), 11(27), 12(38), 13(52), 14(47), 15(26), 16(20), 17(19), 18(3), 19(2), 20(1); scale rows between origin of pelvic fin and lateral line: 8(15), 9(44), 10(51), 11(55), 12(29), 13(24), 14(7), 15(2); scale rows around caudal peduncle above lateral line: 12(9), 13(20), 14(26), 15(49), 16(44), 17(32), 18(14), 19(18), 20(13), 21(3); scale rows around caudal peduncle below lateral line: 10(2), 11(8), 12(15), 13(43), 14(43), 15(42), 16(31), 17(29), 18(7), 19(6), 20(2); dorsal fin rays: 7(5), 8(239), 9(2); anal fin rays: 6(2), 7(188), 8(50), 9(3); pectoral fin rays: 14(16), 15(92), 16(90), 17(40), 18(3); pelvic fin rays: 7(4), 8(49), 9(2); supratemporal pores: 4(3), 5(20), 6(23), 7(9), 8(3); supraorbital pores: 5(1), 7(4), 8(28), 9(20), 10(5); infraorbital pores: 15(8), 16(13), 17(12), 18(15), 19(4), 20(5); preoperculo-mandibular pores: 8(2), 9(5), 10(56), 11(71), 12(44), 13(1), 14(1); total vertebrae: UMMZ 172238, trib. Río Grande de Santiago, 36(3), 37(20), 38(8); UMMZ 172050, trib. Río Chila N Compostela, 37(11), 38(16), 39(3); UMMZ 172042, Arroyo de Mazatán (trib. Río Chila S Compostela), 36(17), 37(11).

Teeth 4-4; ratio of anterior to posterior arm length less than 1.2. Scales with radii on all fields.

Maximum standard length about 95 mm. Proportional measurements for the holotype and 23 paratopotypes are given in Table 4.

TABLE 3
TOTAL NUMBER OF GILL RAKERS ON THE FIRST BRANCHIAL ARCH IN FIVE SPECIES OF THE GENUS *ALGANSEA*

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	N	\bar{X}	
<i>Algansea monticola monticola</i>																									
Jalisco-Zacatecas: Ríos Juchipila and Colotlán ¹		9	70	77	64	12	2																234	8.0	
<i>Algansea monticola avia</i>																									
Nayarit ²	4	34	80	48	15	4																	185	7.3	
<i>Algansea aphanea</i>																									
Jalisco: Río Ayutla (UMMZ 192196)		3	11	14	6	1																	35	7.7	
<i>Algansea barbata</i>																									
México: Valley of Toluca (see text)			2	3	1	1																	7	8.1	
<i>Algansea tincella</i>																									
Jalisco: Río Verde Basin ³									2	9	12	21	12	3	1									60	15.7
Jalisco: Río Ameca Basin ⁴								1	24	30	22	8	3											88	14.2
Jalisco: Lake Zacoalco (TU 30751)												2	1	7	6	5	8	2						31	19.4
Jalisco: Lake Sayula (UMMZ 192246)										2	7	13	6	2										30	16.0
Jalisco: Lake Chapala Basin ⁵														6	9	7	30	12	13	3	4	1		85	21.3
Michoacán: Valley of Tocuambo (UMMZ 189608, 192437)									7	25	15	5												52	15.3
Michoacán: Near Maravatío ⁶					1	9	24	13	2															49	12.1
Michoacán: Río de Morelia, Undameo (UMMZ 178582)				2	10	8	3		2		1													26	11.0
Querétaro: Río San Juan del Río (TU 31876, USNM 55746)									3	9	5	5	1											23	14.6
San Luis Potosí: SW Jesús María (UMMZ 189577)											2	8	20	3	2									35	16.8
Federal District: Valley of México ⁷									1	8	15	6	2											32	15.0
<i>Algansea lacustris</i>																									
Michoacán: Lake Pátzcuaro ⁸														2	12	11	12	2	1					40	20.1

¹ Based on Barbour and Contreras, 1968.

² Based on UMMZ 172042, 172047, 172050, 172112, 172238, 178311.

³ Based on TU 30704, UMMZ 161663.

⁴ Based on UMMZ 172220, 178319, 192173.

⁵ Based on TU 31962; UMMZ 108643, 124458, 167677, 179710, 179734, 179752, 189276.

⁶ Based on P 949, 962; UMMZ 192391.

⁷ Based on UMMZ 192561, 192562; USNM 48211, 55746, 55747; FMNH 3683, 3689, 4527, 4529.

⁸ Based on P 2151; TU 30835; UMMZ 154353, 189275, 192560; USNM 55765, 130208; FMNH 3630.

TABLE 4
 PROPORTIONAL MEASUREMENTS OF TWO SPECIES OF THE GENUS *ALGANSEA*
 EXPRESSED AS PERCENTAGES OF THE STANDARD LENGTH (MEANS IN PARENTHESES)

Number of specimens	<i>A. monticola avia</i> ¹				<i>A. aphaneta</i> ²				
	Holo-type	10 Males	14 Females	Holo-type	14 Males	10 Females	Holo-type	14 Males	10 Females
Standard length	73.4	61.3-67.9 (64.0)	64.1-84.5 (72.4)	83.3	64.5-77.0 (69.7)	71.9-83.3 (76.3)			
Head length	26.8	25.1-27.0 (26.0)	24.9-29.0 (26.7)	23.8	23.1-25.9 (24.2)	23.4-25.2 (24.4)			
Postorbital head length	14.3	12.8-14.4 (13.5)	12.9-15.5 (14.1)	10.9	10.5-12.5 (11.5)	10.9-12.5 (11.8)			
Orbit length	4.8	4.7-5.9 (5.1)	4.6-5.3 (4.8)	5.0	5.0-6.0 (5.5)	4.8-5.3 (5.1)			
Snout length	9.0	7.6-9.0 (8.3)	7.9-10.0 (8.8)	8.8	7.4-9.0 (8.1)	7.6-9.2 (8.6)			
Upper jaw length	7.2	6.6-7.4 (6.8)	6.2-8.3 (7.1)	6.6	5.5-6.7 (6.3)	5.8-7.2 (6.5)			
Mandible length	8.2	7.5-9.0 (8.3)	8.0-9.7 (8.5)	7.4	6.8-8.8 (7.9)	6.8-8.4 (7.6)			
Interorbital width	10.4	9.5-10.6 (9.8)	9.5-10.9 (10.1)	8.4	8.3-9.7 (9.0)	8.3-9.9 (9.0)			
Predorsal length	53.4	51.2-54.5 (52.7)	51.4-55.6 (53.5)	51.4	50.0-55.6 (51.5)	51.0-52.3 (51.8)			
Prepelvic length	53.0	51.0-53.1 (51.8)	51.1-54.8 (52.9)	48.4	46.1-50.1 (47.7)	46.7-48.6 (47.7)			
Preal length	70.7	67.7-70.9 (70.1)	69.7-74.4 (71.6)	66.6	63.5-71.0 (66.2)	66.2-68.2 (67.0)			
Greatest body depth	24.8	21.3-24.1 (22.9)	20.5-24.8 (22.6)	23.4	22.2-24.7 (23.3)	21.0-24.5 (22.6)			
Occipital depth	18.4	16.1-18.7 (17.4)	16.0-18.4 (17.3)	15.8	15.8-18.1 (17.0)	15.1-17.4 (16.4)			
Caudal peduncle length	22.3	21.8-24.5 (22.9)	20.6-23.9 (22.6)	23.8	19.2-26.0 (24.5)	22.3-24.7 (23.8)			
Least depth	11.8	11.3-12.8 (12.2)	10.8-12.6 (11.6)	10.4	10.4-11.5 (11.0)	9.4-11.3 (10.4)			
Dorsal fin, basal length	10.4	8.5-10.7 (10.0)	8.8-10.9 (9.6)	10.1	9.2-11.0 (10.0)	9.1-10.7 (9.9)			
Depressed length	18.1	18.0-20.0 (19.2)	16.8-19.3 (18.0)	19.7	20.5-22.8 (22.0)	19.7-21.0 (20.3)			
Anal fin, basal length	7.9	7.2-8.0 (7.7)	6.2-7.9 (7.2)	9.4	8.3-10.4 (9.6)	8.8-10.2 (9.5)			
Depressed length	14.6	14.7-16.6 (15.8)	13.6-15.7 (14.6)	16.7	17.0-19.2 (18.1)	16.1-17.2 (16.6)			
Pectoral fin length	16.1	17.5-20.0 (18.8)	14.2-18.3 (15.8)	16.2	17.1-21.8 (20.8)	15.4-17.9 (16.7)			
Pelvic fin length	12.3	12.6-14.4 (13.6)	11.2-13.4 (12.4)	13.2	13.8-16.3 (15.3)	13.0-13.8 (13.5)			

¹ Based on UMMZ 193378, 172238.

² Based on UMMZ 193377, 192196.

Sexual dimorphism was noted in the depressed lengths of the dorsal and anal fins and in the lengths of the pectoral and pelvic fins.

Body form and pigmentation pattern are shown in Fig. 4. Dorsum of snout, head, and body dark brown or olive brown. Anteriorly, melanophores encircle eye, usually include infraorbital canal, and extend posteriorly across dorsal half or third of cheek. Posterior to head dorsolateral scale margins and/or myomeres may be outlined by melanophores; dark, narrow middorsal longitudinal stripe usually present. Ventral half of body creamy white to metallic silver.

Melanophores usually sparsely distributed over rays and interradi al membranes of dorsal, anal, and caudal fins (see also Diagnosis), concentrated along ray margins. Except for caudal fin, pigment cells tend to be most dense at fin bases. Pigmentation on pectoral fin usually concentrated along anterior margin of first ray, distributed as on median fins over rays and interradi al membranes, becoming very sparse posteriorly. Anterior rays of pelvic fins may also be lightly sprinkled with melanophores.

Small, fleshy, recurved nuptial tubercles present on dorsal surface of rays 2 to 9 of pectoral fin; a single file of one tubercle per segment on the outer two-thirds of rays 2 and 3 and on the outer three-fourths of rays 4 to 9. The files may branch once. Small tubercles on the dorsum of the head tend to be clustered in the region of the supraorbital canal. None was found on the remaining surfaces of the head, the remaining fins, or on the body.

Preethmoids ossified; supraethmoid rectangular, with single anterior notch. Anterior margin of frontals sharply convex along sutures with supraethmoid and lateral ethmoids as compared to *A. aphanea* and large *A. tincella* and *A. popoche* (Figs. 9B, 10). Concave orbital margins containing supraorbitals (not shown) formed by posterolateral margins of lateral ethmoids and anterolateral margins of frontals. Posteriorly, frontal margins angle ventrally to meet lateral projections of the sphenotics forming a shelf lateral to the anterior part of the lateral temporal fossae. Parietals usually excluded from contact with the sphenotics by frontal-pterotic articulations; in one specimen (Fig. 9A) exposed portions of the sphenotics lie at the anterolateral corners of the parietals, separating the frontals from the pterotics. Spine-like processes of the pterotics well developed, projecting posteriorly and ventrally from posterolateral corners of neurocranium. Convex posterior surfaces of epiotics smoothly crescent-shaped, extend laterally from supraoccipital, curving ventrally just mesial to posttemporal fossae and ending on exoccipitals. Weak eave-like arches extend horizontally across epiotics. Lateral wings of exoccipitals enlarged mesially. Pharyngeal process of basioccipital descends obliquely from skull, often slightly recurved posteriorly to parallel vertebral column, as in *A. tincella* (Fig. 12A); relatively long, slender, flattened distally to form narrow vertical paddle;

ventral masticatory surface roughly pentagonal in outline, flat or slightly concave, about one-half to one-third of surface beneath skull.

Infraorbital series enlarged except for two or three bones posterior to lachrymal; number of separate elements usually 5 or 6; dermosphenotic plate-like.

Quadrate delicate, anterior part flat, fan-shaped, ventral process produced posteriorly into long, handle-like strut.

Mandibles relatively stout, forming oval outline; biting edge of gnathic rami slightly deflected laterally, as in *A. tincella* (Fig. 14A).

Urohyal variable, tear-drop shaped, with moderately long and delicate anterior fork in specimens from northern part of species range; individuals examined from the Río Chila basin have short, stout urohyals characteristic of *A. aphaea* (Fig. 15C).

Maxilla as in *A. tincella*; rostral process slopes sharply away from palatine process ventromesially; articular facet on palatine process moderately to well developed; premaxillary process usually short. Least depth of maxilla between ascending and palatine processes about one-half distance between midpoints of these processes when stepped off along the curvature of the bone (Fig. 16A).

VARIATION.—Variability between populations of *A. m. avia* is best illustrated by the consistent pattern of differences in the number of median lateral scales (Table 1). Relatively large scales are found in specimens from the tributary to the Río Chila (UMMZ 172050, 192188) just north of Compostela, whereas smaller scales characterize the population found at the type-locality in the tributary to the Río Grande de Santiago near Santa María (UMMZ 172238). The remaining populations fall between these two extremes although the northern collections tend to have more numerous scales than those from the tributaries to the Río Chila south of Compostela (UMMZ 172042, 172112).

The same pattern reoccurs in other meristic characters. In the number of scale rows between the origin of the dorsal fin and the lateral line, the type-series has 14 to 17 scales whereas specimens from north of Compostela have 10 to 13. The remaining samples fall between 11 and 16 for this count. The type-series has 15 to 21 scale rows around the caudal peduncle above the lateral line, whereas fish from north of Compostela have only 12 to 16. The remainder fall between 13 and 19. The types have 36 to 49 predorsal scales and specimens from north of Compostela, 30 to 38. The remainder fall between 31 and 43. The consistent intermediacy of four of the populations sampled precludes taxonomic recognition of the two extremes even though they show no overlap in the number of median lateral scales and in the number of scale rows between the origin of the dorsal fin and the lateral line.

The pattern of variation in the number of vertebrae in the Río Chila is the same; the southern population (UMMZ 172042) has a lower

mode (36) than that from north of Compostela (UMMZ 172050, 38), whereas the type-series is intermediate (37). The reason for this variation is unknown.

ECOLOGY.—The type-series was taken in moderately swift water up to one meter deep over bedrock, rocks, and gravel, or around boulders. Vegetation consisted of green algae. Associated species were *Poeciliopsis viriosa* Miller and *Xenotoca eiseni* (Rutter). At other localities, *A. m. avia* was associated with *Ictalurus* sp., *Goodea atripinnis* Jordan, *Poecilia butleri* Jordan, and *Cichlasoma* sp., usually with the same type of habitat but with greater plant diversity.

Adults of both sexes collected between mid-February and mid-April had well-developed gonads, indicating that spawning occurs during the early spring.

REMARKS.—Although the ranges of *A. m. avia* and *A. m. monticola* are separated by a distance of approximately 130 km as well as the deep barranca of the Río Grande de Santiago, there has apparently not been sufficient time or selection pressure for them to become reproductively isolated from each other. Both forms overlap to a slight degree in all diagnostic characters and in their time of spawning. As stated above, *A. m. avia* appears to be reproductively active between mid-February and mid-April. Ovigerous females of *A. m. monticola* have been collected between the first of April and early July. For these reasons we consider the two forms to be recognizable at the subspecific level only.

Final geographic separation of the two forms probably occurred during the mid-Pleistocene uplift when the barranca of the Río Grande de Santiago was formed. Thus, knowledge of the age of the barranca would yield interesting information regarding the rate of morphological differentiation within the species. We note, however, that any conclusions drawn from such data should be regarded as a rough approximation since nothing is known about geographic variation within the ancestral species.

ETYMOLOGY.—The subspecific name is derived from the Latin *avius* meaning out of the way or remote, and refers to the fact that the subspecies occupies the westernmost part of the range of the genus.

Algansea monticola monticola Barbour and Contreras
Fig. 5A

Algansea monticola Barbour and Contreras, 1968:101, fig. 1 (original description, type-locality: Río Juchipila at hwy 70 bridge, 1.6 km E jct. with hwy 41, NE Jalpa, Zacatecas). Alvarez, 1970: 58 (key).

RANGE.—Headwaters of the ríos Colotlán and Juchipila, northern tributaries to the Río Grande de Santiago, in Zacatecas and Jalisco (Fig. 2).

DIAGNOSIS.—Barbels present; gill rakers 6 to 11; gut in the form of a simple loop (as in Fig. 3A), occasionally with slight secondary flexure (as in Fig. 3B); black spot at base of caudal fin does not extend out



Fig. 5. Two species of *Algansea*: (A) *A. monticola monticola*, male, 56.0 mm, UMMZ 189064; (B) *A. barbata*, male, 103.2 mm, P 966.

onto median caudal rays or interradiial membranes; weak median lateral stripe set off from dark dorsum by a light band equal to width of eye; scattered melanophores ventral to lateral stripe usually do not extend to pelvic fins; dorsal rays (213 specimens), 7(192), 8(21); mouth terminal, upper lip not overhung by snout. Minute nuptial tubercles may be aligned along posterior margins of pectoral fin rays.

DESCRIPTION.—Number of median lateral scales, gill rakers, and total number of preoperculomandibular pores are given in Tables 1-3. Other counts follow. Predorsal scales: 29(2), 30(4), 31(5), 32(6), 33(5), 34(4), 35(2), 36(1), 37(1); scale rows between origin of dorsal fin and lateral line: 11(1), 12(8), 13(16), 14(5), 15(1); scale rows between origin of pelvic fin and lateral line: 6(1), 7(4), 8(7), 9(11), 10(6), 11(2); scale rows around caudal peduncle above lateral line: 14(3), 15(14), 16(10), 17(3); scale rows around caudal peduncle below lateral line: 11(1), 12(6), 13(6), 14(11), 15(5); dorsal fin rays: 7(213), 8(21); anal fin rays: 6(8), 7(217), 8(5); pectoral fin rays 11(1), 13(1), 14(2), 15(42), 16(113), 17(56), 18(5); pelvic fin rays: 7(3), 8(25), 9(2); supratemporal pores: 4(1), 5(7), 6(6), 7(10), 8(11), 9(5); supraorbital pores: 7(2), 8(19), 9(10), 10(9); infraorbital pores, left side: 14(2), 15(7), 16(12), 17(11), 18(7), 19(1), right side: 11(1), 14(1), 15(4), 16(9), 17(13), 18(7), 19(2), 20(3); preoperculomandibular pores: 9(3), 10(11), 11(16), 12(5), 13(5), 14(1); total vertebrae: 33(3), 34(1), 35(6), 36(40), 37(25), 38(2).

TABLE 5
 PROPORTIONAL MEASUREMENTS OF FIVE SPECIES OF THE GENUS *ALGANSEA*
 EXPRESSED AS PERCENTAGES OF THE STANDARD LENGTH (MEANS IN PARENTHESES)

	<i>A. tincella</i> ¹ 181	<i>A. lacustris</i> ² 5	<i>A. popoche</i> ³ 24	<i>A. barbata</i> ⁴ 5	<i>A. monticola</i> <i>monticola</i> ⁵ 15
Number of specimens	181	5	24	5	15
Standard length	60.7-125.8 (79.2)	149.7-168.3 (157.7)	83.9-98.5 (92.8)	78.5-108.6 (95.9)	55.9-70.2 (62.0)
Head length	23.7-29.0 (26.4)	25.7-26.2 (26.0)	28.2-31.2 (29.8)	20.6-27.8 (25.1)	24.9-28.5 (25.8)
Postorbital head length	13.1-17.0 (15.0)	14.4-15.0 (14.6)	15.0-18.0 (16.6)	11.5-15.8 (14.3)	13.2-15.3 (14.0)
Orbit length	3.7-6.6 (4.9)	3.8-4.3 (4.1)	4.8-6.2 (5.4)	3.6-4.3 (4.0)	4.5-5.6 (4.9)
Snout length	6.1-8.5 (7.2)	7.4-8.3 (7.9)	8.1-9.3 (8.7)	6.1-8.4 (7.5)	6.7-7.9 (7.2)
Upper jaw length	5.5-8.0 (6.6)	5.9-7.0 (6.4)	7.7-9.2 (8.2)	4.3-6.8 (5.8)	5.7-7.4 (6.5)
Mandible length	6.6-9.8 (8.3)	8.4-8.6 (8.5)	10.3-12.0 (11.0)	6.0-7.7 (7.2)	7.6-9.2 (8.2)
Interorbital width	8.2-10.7 (9.4)	9.1-10.3 (9.5)	10.8-12.2 (11.5)	6.7-9.3 (8.2)	8.3-10.4 (9.2)
Predorsal length	49.2-56.8 (52.6)	50.8-54.0 (52.7)	48.0-52.4 (50.8)	42.8-59.3 (52.9)	52.2-56.6 (54.6)
Prepelvic length	48.8-55.6 (52.3)	52.5-53.5 (53.1)	49.7-52.0 (51.0)	41.9-59.0 (52.0)	50.7-53.7 (52.5)
Prealanal length	67.6-77.0 (72.5)	72.3-76.5 (74.0)	68.8-71.6 (70.3)	56.4-80.9 (70.5)	69.0-74.4 (71.4)
Greatest body depth	19.9-33.0 (24.7)	21.9-24.7 (23.1)	19.5-22.4 (21.1)	19.2-26.5 (23.6)	23.0-28.9 (26.0)
Occipital depth	15.1-24.0 (17.4)	16.4-18.2 (17.6)	16.5-18.6 (17.7)	13.8-17.7 (16.2)	16.6-18.6 (17.6)
Caudal peduncle length	18.4-24.7 (21.3)	19.0-23.1 (21.4)	21.6-25.1 (23.0)	16.3-21.9 (19.4)	19.8-24.0 (21.8)
Least depth	11.1-14.8 (12.7)	10.9-12.4 (11.5)	10.6-11.9 (11.4)	10.0-13.6 (12.1)	12.6-14.3 (13.4)
Dorsal fin, basal length	6.3-12.1 (9.9)	8.2-10.5 (9.4)	9.4-10.9 (10.2)	7.8-10.7 (9.0)	9.0-10.6 (10.0)
Depressed length	16.3-23.0 (20.1)	16.8-18.1 (17.3)	20.9-23.2 (22.0)	15.9-20.0 (17.7)	19.7-23.3 (21.3)
Anal fin, basal length	5.8-11.5 (7.4)	6.2-7.4 (7.0)	7.1-8.5 (7.7)	6.7-8.4 (7.5)	7.8-9.2 (8.0)
Depressed length	13.8-18.8 (15.9)	14.2-15.0 (14.6)	15.7-18.7 (17.2)	12.6-15.8 (14.3)	15.7-19.5 (17.7)
Pectoral fin length	12.7-23.3 (17.8)	15.5-17.0 (16.3)	17.3-20.4 (18.8)	12.2-16.3 (15.5)	15.8-22.7 (18.6)
Pelvic fin length	10.6-16.5 (14.1)	12.3-13.0 (12.6)	14.8-16.5 (15.8)	10.2-12.7 (11.5)	13.4-16.4 (14.6)

¹See species description for collections.

²Based on TU 30835 and USNM 131689.

³Based on UMMZ 167717.

⁴Based on P 966.

⁵Based on UMMZ 184357, 184359, 184358, 189064, 192266.

Teeth 4-4; ratio of anterior to posterior arm length less than 1.2. Scales with radii on all fields.

Maximum standard length about 90 mm. Proportional measurements are presented in Table 5.

Color variable, but always dull; dusky gray to gray-brown dorsally, grayish white ventrally. A diffuse rust-orange band may be present between dorsal margin of operculum and midbase of caudal fin; black spot present at latter point.

Minute nuptial tubercles on median portion of dorsal surface of pectoral rays 2 to 10 and on all rays of dorsal and anal fins; scattered on dorsum of head without apparent pattern; present on body along posterior margins of scales dorsally as in *A. tincella*.

Osteology as described for *A. monticola avia*; urohyal tear-drop shaped, similar to that of specimens of *A. m. avia* from the vicinity of Tepic and the type-locality.

ECOLOGY.—Ubiquitous in those parts of the headwaters of the ríos Juchipila and Colotlán sampled. *Algansea m. monticola* was taken over mud, gravel, and rocks, in open water and under banks, in swift water, and in pools and impoundments. Associated native fishes were *Yuriria alta* (Jordan),¹ *Moxostoma congestum* (Baird and Girard), and *Goodea* sp.

Spawning appears to take place between early April and early July.

MATERIAL EXAMINED.—Aguascalientes: UMMZ 189064 (6), Río Calvillo, trib. Río Juchipila, at Calvillo, 1 April 1968. Jalisco: UMMZ 184354 (15), Río Colotlán at Santa María de los Angeles, 27 June 1963. Zacatecas: UMMZ 184353 (5), Río Juchipila about 3.2 km N Momax on road to Colotlán, 27 June 1963; UMMZ 184355 (2), small pool at foot of dam across trib. Río Colotlán, about 3.2 km S Tepetongo, 28 June 1963; UMMZ 184356 (5), trib. Río Juchipila at Mal Paso, about 25.8 km E Ciudad García Salinas, 28 June 1963; UMMZ 184357 (10), trib. Río Juchipila about 8.0 km S Villanueva on hwy 41, 28 June 1963; UMMZ 184358 (3), trib. Río Juchipila at Tabasco, 29 June 1963; UMMZ 184359 (3), Río Juchipila on hwy 70, about 1.6 km E hwy 41, NE Jalpa, 30 June 1963; UMMZ 192260 (18), Río Juchipila just N Santa Rosa (Mezquituta), 30 April 1969; UMMZ 192266 (20), Río Juchipila about 1.6 km NE Jalpa at hwy 70, 30 April 1969. For other material examined, see Barbour and Contreras (1968).

Algansea aphanea, new species

Fig. 6

RANGE.—Known only from the Río Ayutla, a headwater of the Río Armería, and from a tributary to the Río Tuxpan in the Coahuayana basin—both in Jalisco (Fig. 2).

DIAGNOSIS.—Barbels present; gill rakers 6 to 10; gut in the form of a simple loop (as in Fig. 3A); dorsal rays 8; black spot at base of caudal fin set off from lateral stripe by a gap or constriction of the pigment band, the spot extending onto median caudal rays or, occasionally, onto rays and interradiial membranes; dark median lateral stripe set off from dark dorsum by a light band equal to or greater than width of

¹Reasons for recognizing *Yuriria* are given by Miller (1976).



Fig. 6. *Algansea aphanea*: (A) male, 75.9 mm, UMMZ 192196; (B) holotype, female, 83.3 mm, UMMZ 193377.

pupil; scattered melanophores ventral to lateral stripe may extend to pelvic fins; upper lip overhung by snout.

Outline of neurocranium triangular in dorsal view (Fig. 9B); median, narrow supraethmoid tilted strongly anteroventrally; supraorbital rim formed by lateral ethmoids and anterolateral margins of frontals very broadly concave; parietals extend anterolaterally as long finger-like projections between frontals and pterotics, apices meet or nearly meet sphenotics; eave-like arches on epiotics absent or very weakly developed, convex posterior surface of epiotics smoothly crescent-shaped, extend laterally from supraoccipital curving ventrally just mesial to posttemporal fossae and ending on exoccipitals; masticatory surface of basioccipital lies almost entirely beneath skull; infraorbital bones reduced in width and number, usually about 6, dermosphenotic tubular (Fig. 17A); relative lengths of posterior arm of quadrate and symplectic as described for *A. monticola avia*, but much shorter and more massive; biting surfaces of gnathic rami very strongly deflected laterally (Fig. 14C); least depth of maxilla between ascending and palatine processes more than one-half the distance between the midpoints of these processes when stepped off along the curvature of the bone (Fig. 16B).

TYPES.—Holotype, UMMZ 193377, and adult female 83.3 mm from the Río Ayutla, 10 km W of jct. of Mascota road with hwy 80, about 4.8 km SE Ayutla, Jalisco, 22 April 1968, C. D. Barbour and R. J. Douglass. Taken with the holotype were 271 paratopotypes, UMMZ 192196 (221, 22-86 mm, 6 cleared and stained), ANSP 136517 (10, 32.5-78.7 mm), CAS 40708 (10, 30.4-84.2 mm), FMNH 83855 (10, 29.8-84.2 mm), TU 105478 (10, 32.5-78.7 mm), USNM 218275 (10, 29.1-83.1 mm). Additional paratopotypes from the same locality are UMMZ 178363 (78, 39-79 mm, 3 cleared and stained), 7 March 1957, R. R. and M. Miller.

ADDITIONAL SPECIMENS.—Jalisco: UMMZ 172151 (32, 17-31 mm), trib. Río Tuxpan, 8.0 km N Pihuamo, 8 March 1955; UMMZ 189599 (1, 82 mm) and UMMZ 198838 (7, 48-69 mm), Río Terrero, 0.8 km W 21 de Noviembre (on hwy 110, 16 km N Pihuamo), 24 February 1970 and 18 February 1976.

DESCRIPTION.—Holotype with 78 median lateral scales and 10 (including 2 rudimentary) gill rakers on the first arch. Frequency distributions for these characters and the total number of preoperculomandibular pores are given in Tables 1-3. Other counts based on UMMZ 192196 follow; those that include the holotype are italicized. Predorsal scales: 38(1), 39(5), 40(2), 41(5), 42(4), 43(6), 44(5), 47(1), 49(1); scale rows between origin of dorsal fin and lateral line: 13(1), 14(2), 15(6), 16(8), 17(12), 18(3), 19(2), 20(1); scale rows between origin of pelvic fin and lateral line: 11(4), 12(6), 13(13), 14(6), 15(1); scale rows around caudal peduncle above lateral line: 16(1), 17(3), 18(3), 19(10), 20(11), 21(2); scale rows around caudal peduncle below lateral line: 15(1), 16(6), 17(12), 18(3), 19(6), 20(2); dorsal fin rays: 8(35); anal fin rays: 7(2), 8(30), 9(3); pectoral fin rays: 14(5), 15(26), 16(2), 17(2); pelvic fin rays: 7(1), 8(41); supratemporal pores: 4(1), 5(7), 6(11), 7(3); supraorbital pores: 8(7), 9(9), 10(6); infraorbital pores: 14(1), 15(2), 16(10), 17(8), 19(1); preoperculomandibular pores: 8(3), 9(12), 10(13), 11(4); total number of vertebrae: 38(5), 39(24), 40(3).

Teeth 4-4; ratio of anterior to posterior arm length less than 1.2. Scales with radii on all fields.

Maximum standard length about 86 mm. A summary of proportional measurements for the holotype and 23 paratopotypes is given in Table 4. Sexual dimorphism was noted only in the lengths of the pectoral and pelvic fins.

Body form and pigmentation pattern (Fig. 6) are similar to *A. monticola avia* and to darker individuals of *A. tincella*, particularly those from the Río Teuchitlán (UMMZ 172220). Color in life dark brown or olive-brown dorsally, creamy white to metallic silver ventrally.

Small, recurved nuptial tubercles aligned one per ray segment are present on rays 2 to 10 or 11 of pectoral fin; they occur along the entire lengths of rays 2 to 8 but are restricted to the more distal portions of rays 9 to 11. The files appear to branch only once. Tubercles also present on the dorsum of the head as described for *A. tincella* and on pelvic rays 2 to 4. None found on the dorsal, anal, or caudal fins or on the body.

Roof of neurocranium domed as in *A. monticola avia*; preethmoids ossified; median, narrow supraethmoid V-shaped in cross-section, longer than wide, mesial part of leading edge forms short, pointed projection; anterior margin of frontals sharply convex; blunt lateral projections of the sphenotics smoothly in line with the outline of the frontals; shelves lateral to anterior part of lateral temporal fossae broad; spine-like processes of pterotics well developed, project backward and downward from posterolateral corners of neurocranium; exoccipital bridges dorsal

to lateral occipital foramina more robust than in *A. tincella*, but not as extreme as in *A. popoche*; mesial portions of exoccipital wings ventral to lateral occipital foramina slender as in *A. tincella*. Masticatory surface of basioccipital as described for *A. tincella*; posterior portion of pharyngeal process short, paddle-shaped.

Mandible relatively short and stout as in *A. tincella*, enlarged at symphysis. Articular facet of articular large and posteriorly directed (Fig. 14C; this characteristic is highly variable in *A. tincella*, and probably in all other species of the genus as well).

Urohyal short, very broad; arms of anterior bifurcation curved mesially (Fig. 15C).

Relatively short rostral process of maxilla extends mesially and slightly ventrally from palatine process; articular condyle on palatine process large; premaxillary process large, easily seen extending beyond rostral process when maxilla is viewed mesially (Fig. 16B).

ECOLOGY.—*Algansea aphanea* is an inhabitant of swift currents in water deeper than 0.7 meters. In the Río Ayutla it was usually taken below falls and in riffles where the bottom was characterized by gravel and rocks. The water was clear and the only aquatic plants observed were green algae. Other species taken in the same collection were *Moxostoma* sp., *Ilyodon* sp., and the introduced *Lepomis macrochirus* Rafinesque. The centrarchid was nesting in the quieter waters of the river. In the Río Tuxpan basin it was associated with *Allodontichthys tamazulae* Turner and two undetermined species of *Ilyodon*.

Gonadal development in specimens from the Río Ayutla suggests that spawning begins during the end of April or in early May.

ETYMOLOGY.—The specific name *aphanea* is derived from the Greek *αφανης*, meaning secret or unknown, and refers to the considerable osteological differences separating it from the other barbeled species of *Algansea*.

Algansea barbata Alvarez and Cortés

Fig. 5B

Algansea barbata Alvarez and Cortés, 1964:104, fig. 1 (original description, type-locality: Río Lerma at Lerma, State of México). Romero, 1967:49 (additional localities). Alvarez, 1970:58 (key).

RANGE.—Headwaters of the Río Lerma, in and near the Valley of Toluca, State of México (Fig. 2).

DIAGNOSIS.—Barbels present; gill rakers 7 to 10; dorsal rays usually 8; anteriorly directed single loop of the gut folded posterolaterally in a counter-clockwise direction (Fig. 3B); median lateral stripe very poorly defined, separation from grayish brown dorsum vaguely apparent in region of caudal peduncle; scattered melanophores on ventral half of body usually do not extend to pelvic fins; mouth subterminal, upper lip

overhung by snout. Blunt posterolateral projections of frontals, which limit concave supraorbital margins posteriorly, are expanded.

DESCRIPTION.—Number of median lateral scales, gill rakers, and total number of preoperculomandibular pores are given in Tables 1-3. The first two frequency distributions also include counts for these characters given by Alvarez and Cortés (1964). All other data, including those that follow, are derived only from specimens that we have examined. Predorsal scales: 45(1), 50(2), 51(1), 52(1), 54(1), 56(1); scale rows between origin of dorsal fin and lateral line: 19(2), 20(2), 21(1), 22(2); scale rows between origin of pelvic fin and lateral line: 14(2), 15(1), 16(1), 17(1), 20(1), 21(1); scale rows around caudal peduncle above lateral line: 24(1), 25(2), 29(1); scale rows around caudal peduncle below lateral line: 23(1), 24(3); dorsal fin rays: 8(7); anal fin rays: 7(5), 8(1), 9(1); pectoral fin rays: 15(2), 16(3), 17(1), 18(1); pelvic fin rays: 8(5); supratemporal pores: 15(2), 16(3), 17(1), 18(1); supraorbital pores, left side: 7(1), 9(2), 10(3), 12(1), right side: 8(1), 9(2), 10(3), 11(1); infraorbital pores, left side: 18(2), 19(4), 21(1), right side: 16(1), 17(2), 18(1), 20(1), 21(1), 23(1); preoperculomandibular pores, left side: 10(1), 11(1), 12(2), 13(1), 14(2), right side: 10(1), 12(3), 13(2), 14(1); total vertebrae, 38(3), 39(1).

Teeth 4-4; scales with radii on all fields.

Maximum standard length about 130 mm. A summary of proportional measurements for *A. barbata* is presented in Table 5.

The pigmentation pattern (based on preserved material) is similar to that of *A. tincella* from the tributaries to the Río Verde: almost uniform gray or gray-brown dorsally and white or gray-white ventrally. As mentioned in the diagnosis, the median lateral stripe is very faint. The spot at the midbase of the caudal fin is present in juveniles but appears to be absent in adults of this species (Alvarez and Cortés, 1964; our observations).

Small, recurved or blunt nuptial tubercles present on all fins except caudal; arranged in single rows along the rays, usually with one tubercle per ray segment. The files may branch twice. Tubercles most highly developed on the dorsal surface of the pectoral fins where they are present on the outer one-half of rays 2 to 4 and the outer three-fourths of rays 5 to 10. Tuberculation weak on other fins, present on the outer three-fourths of pelvic rays 2 to 5, the branching segments of anal rays 2 to 7, and on the branching segments of dorsal rays 2 to 8. Tubercles may also be present on the outer one-half of the first dorsal ray.

Outline of neurocranium subtriangular in dorsal view, as in *A. monticola avia* (Fig. 9A), the roof broadly flattened; preethmoids ossified; supraethmoid much longer than wide, directed sharply anteroventrally, median dorsal depression shallow, forming obtuse angle in cross section; anterior margin rounded in dorsal view, mesial notch weakly developed.

Blunt posterolateral projections of frontals form wide shelf lateral to anterior part of lateral temporal fossae. Parietals excluded from contact with sphenotics by frontal-pterotic articulations. Posterior surface of neurocranium as in *A. monticola avia*. Pharyngeal process posterior to masticatory surface variable in length, not recurved.

Quadrate more robust than in *A. monticola avia*.

Mandible as in *A. monticola* and *A. tincella* (Fig. 14A), except for anterolateral edge of gnathic ramus which is intermediate between that of these species and *A. aphaenea*.

Urohyal as in *A. tincella* (Fig. 15B).

Maxilla as in *A. tincella* (Fig. 16A) but with a larger articular condyle on palatine process and wider, more robust rostral process.

ECOLOGY.—*Algansea barbata* lives in standing water or in streams of slow to moderate current where the bottom is sandy silt, mud, or firm clay, and aquatic vegetation is rather sparse; water depths may be at least as great as 1.3 m in lakes or reservoirs. The species spawns during July; ripe, tuberculate specimens (P 966) were collected on 23 July 1966.

MATERIAL EXAMINED.—State of México: UMMZ 97442(2), 97443(1), headwaters of the Río Lerma, near Lerma, at trout hatchery, 15 May 1930; UMMZ 182347(1), paratype, lagoon on trib. Río Lerma, km 100 on hwy 15, 3 March 1947; UMMZ 193481(1), reservoir near Tabernillas, just NE hwy 15, 30 km NW Toluca (close to locality for UMMZ 182347), 11 December 1972; P 966(5) and UMMZ 194166 (2 cleared and stained), Ixtlahuaca (on hwy 55 NNW Toluca), 23 July 1964.

Algansea tincella (Valenciennes)

Fig. 7

Leuciscus tincella Valenciennes, in Cuvier and Valenciennes, 1844:323 (original description, type-locality: México). Günther, 1868:244 (description).

Algansea tincella, Girard, 1856:183 (description); 1859:46, pl. 27, figs. 1-4 (description, adult and scales illustrated). Jordan and Everman, 1896:211 (description). Jordan and Snyder, 1900:120 (description of specimens from Río Verde, Aguascalientes). Eigenmann, 1909:303 (listed). Meek, 1904:44 (synonymy, description). Regan, 1906-08:151 (synonymy, description). Fowler, 1924:391 (description). De Buen, 1946b:109 (synonymy, range). Alvarez, 1950:48 and 1970:59 (keys). Alvarez and Navarro, 1957:19 (synonymy, description).

Leucus tincella, Jordan and Gilbert, 1883:245 (description).

Algansea dugesi Bean, 1892:283, pl. 44, fig. 1 (original description, type-locality: syntypes from the City of Guanajuato and Lake Yuriria, State of Guanajuato). Eigenmann, 1909:303 (listed).

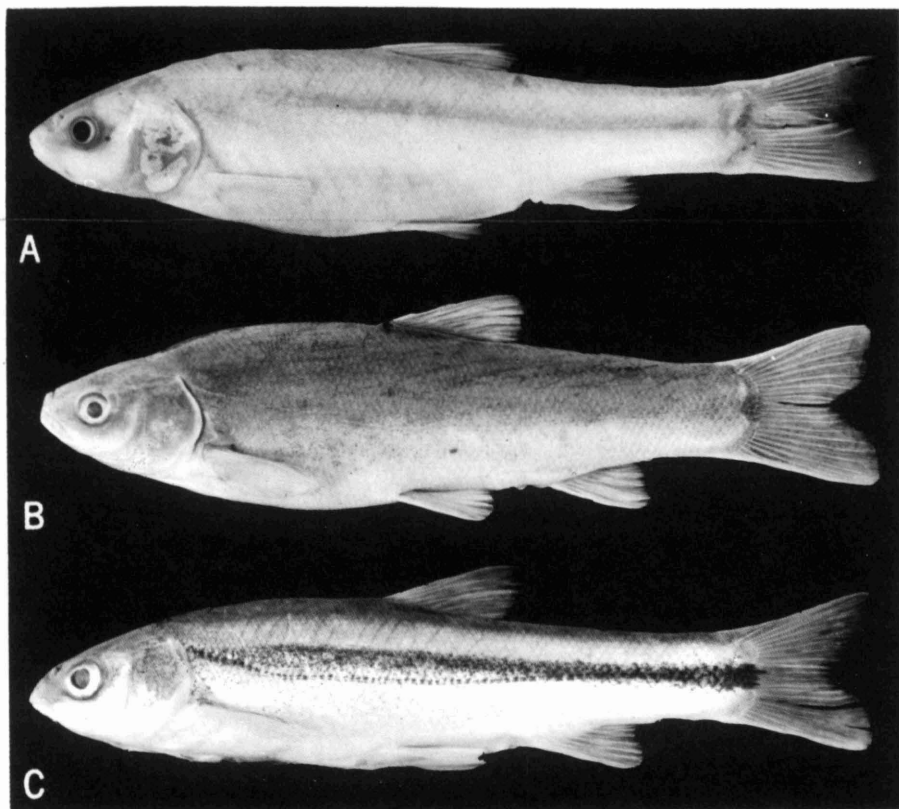


Fig. 7. *Algansea tincella*, showing variation in pigmentation pattern: (A) female, 79.5 mm, TU 30704; (B) male, 110.6 mm, UMMZ 179752; (C) male, 65.4 mm, UMMZ 172220.

Algansea rubescens Meek, 1902:78 (original description, based in part on hybrid [see *Algansea popoche*, Hybridization], type-locality: Río Grande de Santiago at Ocotlán, Jalisco). Eigenmann, 1909: 304 (listed).

Algansea affinis Regan, 1906-08:151, pl. 25, fig. 1 (original description, type-locality: syntypes from Río Verde at Aguascalientes, Aguascalientes, Río Lerma and canals at Salamanca, Guanajuato, and Río San Juan del Río at San Juan del Río, Querétaro).

Algansea stigmatura Regan, 1906-08:152, pl. 25, fig. 2 (original description, type-locality: Río Grande de Santiago).

Leuciscus nigrescens Meek (not of Girard), 1908:153-54 (misidentification; San Miguel, Guanajuato, and Jesús María, S.L. Potosí).

Algansea paratincella Alvarez, 1963:115 (original description, type-locality: San Juanico Reservoir, near Cotija, Michoacán).

Algansea alvarezii Romero, 1967:49, fig. 1 (original description, type-locality: Maravatio de Ocampo, Michoacán).

RANGE.—Widespread on the Mesa Central in the Río Lerma basin and contiguous basins from the Valley of México in the east to lakes Magdalena, Atotonilco, and Sayula in the west. Occurs also on the Atlantic slope in the Río San Juan del Río, Querétaro, and the Río Santa María, San Luis Potosí, both headwaters of the Río Pánuco, and on the Pacific slope (in addition to the Lerma basin) in a tributary to the Río Balsas south of Tocombo, Michoacán, and in the headwaters of the Río Ameca. The species is also present in the tributaries of the Río Verde, the first major northern tributary to the Río Grande de Santiago (Fig. 2).

DIAGNOSIS.—Barbels absent; gill rakers 9 to 25; median lateral scales 52 to 85 (modal number between 65 and 70); scales with radii on all fields; gut forms counter-clockwise flexure with apex directed posteriorly or laterally across the ventral side of the body cavity (Fig. 3C,D), directed anteriorly in only one population examined; adults usually bicolored, in life gray to red-brown or dark brown dorsally, dirty gray to metallic silver ventrally; mouth upturned in large adults (130 mm or more).

DESCRIPTION.—Number of median lateral scales, gill rakers, and preoperculomandibular pores are given in Tables 1-3. Other counts from over the entire range of the species follow. Predorsal scales: 23(1), 24(6), 25(7), 26(7), 27(12), 28(17), 29(27), 30(19), 31(41), 32(38), 33(49), 34(33), 35(32), 36(32), 37(23), 38(7), 39(8), 40(7), 41(5), 42(2), 43(1); scale rows between origin of dorsal fin and lateral line: 10(3), 11(3), 12(17), 13(23), 14(60), 15(66), 16(75), 17(22), 18(5), 19(1); scale rows between origin of pelvic fin and lateral line: 7(11), 8(35), 9(89), 10(94), 11(32), 12(12), 13(1), 14(1); scale rows around caudal peduncle above lateral line: 12(2), 13(9), 14(14), 15(22), 16(25), 17(47), 18(23), 19(39), 20(13), 21(12), 22(6), 23(1), 24(1), 26(1); scale rows around caudal peduncle below lateral line: 10(3), 11(5), 12(9), 13(16), 14(23), 15(42), 16(47), 17(34), 18(15), 19(10), 20(3), 21(7), 22(1); dorsal fin rays: 4(1), 7(10), 8(377), 9(2); anal fin rays: 6(5), 7(345), 8(26); pectoral fin rays: 14(3), 15(27), 16(106), 17(129), 18(53), 19(12); pelvic fin rays: 8(5), 9(248), 10(23); supratemporal pores: 4(1), 5(1), 6(1), 7(16), 8(44), 9(80), 10(76), 11(23), 12(10), 13(2); supraorbital pores: 8(7), 9(44), 10(54), 11(77), 12(60), 13(9), 14(3); infraorbital pores: 14(1), 16(2), 17(6), 18(36), 19(33), 20(61), 21(52), 22(25), 23(19), 24(12), 25(4), 27(1); preoperculomandibular pores: 9(1), 11(10), 12(49), 13(146), 14(141), 15(91), 16(44), 17(35), 18(15), 19(1); total vertebrae: 36(2), 37(16), 38(112), 39(109), 40(33), 41(6).

Teeth: 4-4 (Figs. 18-19); ratio of anterior to posterior arm length less than 1.2. Scales with radii on all fields.

In streams *A. tincella* commonly reaches a standard length of 60 to 90 mm and in lakes and reservoirs it attains the maximum length for the species, about 175 mm.

Proportional measurements for *A. tincella* throughout its range are presented in Table 5, based on specimens from the following collections:

UMMZ 161663, 3♂♂, 21♀♀, 66.1-95.5 mm; UMMZ 172220, 13♂♂, 11♀♀, 60.7-85.1 mm; UMMZ 175582, 5♂♂, 3♀♀, 71.8-125.8 mm; UMMZ 179752, 8♂♂, 10♀♀, 65.9-99.8 mm; UMMZ 189577, 12♂♂, 12♀♀, 62.5-77.0 mm; UMMZ 189608 and 192437, 5♂♂, 7♀♀, 69.3-99.4 mm; UMMZ 192173, 8♂♂, 8♀♀, 68.4-97.8 mm; UMMZ 192246, 8♂♂, 16♀♀, 78.7-99.3 mm; UMMZ 192391, 3♂♂, 97.4-101.3 mm; FMNH 4529 and 3689, 3♂♂, 4♀♀, 64.1-101.0 mm; TU 30704, 12♂♂, 12♀♀, 71.7-92.9 mm.

Pigmentation and color pattern vary within and between populations, becoming vague and poorly defined in large specimens. Dark median lateral stripe almost always present in small (< 100 mm) individuals, but may be prominent only posterior to dorsal fin; when prominent anteriorly, a short, dark vertical bar may extend ventrally, from just behind opercular opening to insertion of pectoral fin. Concentrations of melanophores around scale pores may cause lateral line to appear as a thin dotted line dipping below anterior half of lateral stripe. Small spot usually present at midbase of caudal fin, may or may not be separated from median stripe by pigment-free area or set off only by a slight constriction, occasionally recognizable only as a darker intensification of pigmentation; spot rarely extends out onto median caudal interradiial membranes (noted only in individuals from the Río Teuchitlán, Jalisco, UMMZ 172220). Median stripe usually limited dorsally by light band, narrowest and best defined posterior to dorsal fin.

Distribution of melanophores as in *A. monticola avia* except as noted. Dorsum of snout, head, and body gray, reddish, or dark brown. Ventral half of body may be brick red, cream, or metallic silver; scattered melanophores may extend to pelvic fins.

Small, fleshy, recurved nuptial tubercles present on all fins except caudal; arranged in single rows on the rays, usually with one tubercle per ray segment. The files appear to branch only once. Tubercles most highly developed on dorsal surface of pectoral fins, usually present on the outer five-sixths of rays 2 to 10, occasionally on the medial and distal portions of ray 1. The one tuberculate female seen conforms to the same pattern, but has smaller tubercles. Small tubercles are scattered over top of head with no apparent pattern, extending ventrally on opercles to about the level of the lower margin of the eye; few or none found on snout anterior to eye. On body, 1 to 4 tubercles present along posterior margin of each scale predorsally, becoming fewer posteriorly and ventrally. None seen on body of female.

Outline of neurocranium subtriangular in dorsal view (Fig. 10A), roof broadly flattened even in small adults (Fig. 12A). Preethmoids ossified. Median, butterfly-shaped supraethmoid projects forward from suture with anterior margins of frontals, horizontal or tilted slightly anteroventrally in sagittal view, in cross section flat or weakly V-shaped or slightly convex (UMMZ 189577), usually longer than wide; mesial part of leading edge of supraethmoid forms relatively narrow, bifurcate projection. Outline of anterior margin of frontals along sutures with supraethmoid and lateral ethmoids as described for *A. monticola avia* in small specimens (Fig. 9A), gently convex in large individuals (Fig. 10A); anterolateral margins of frontals and posterolateral edges of lateral ethmoids complete outline of concave supraorbital margin. Supraorbital margin limited posteriorly by blunt, lateral projections of the frontals (Fig. 10A), more prominent than in *A. monticola avia*, but not as extreme as in *A. barbata*. Posterior to the lateral projections, the frontal margins angle ventrally and meet the stout lateral projections of the sphenotics, forming a broad shelf lateral to the anterior part of the lateral temporal fossae. Parietals excluded from contact with sphenotics by frontal-pterotic articulations. Spine-like processes of pterotics well developed, projecting backward and downward from posterolateral corners of neurocranium; epiotics gently convex, convexities extending medially with decreasing prominences across epiotic-supraoccipital suture and ending in slight concavities lateral to base of supraoccipital crest; major points of attachment of epaxial muscles to back of skull are moderately developed eave-like arches projecting slightly from apices of epiotics. Ventrally, lateral wings of exoccipitals tend to be narrow, widening only to buttress ventral edges of pterotics and epiotics; mesially, exoccipitals reduced to narrow bridges, ventral to epiotic-supraoccipital sutures, by prominent lateral occipital foramina. Pharyngeal process of the basioccipital descends obliquely from skull (Fig. 13A), often slightly recurved to parallel vertebral column; relatively long, slender posteriorly, flattened distally to form narrow vertical paddle; ventral masticatory surface roughly pentagonal in outline, flat or slightly concave; about one-half to one-third of surface lies beneath skull.

Infraorbital series enlarged except for two or three bones posterior to lachrymal; number of separate elements varies from 5 or 6 to 11; dermosphenotic plate-like (Fig. 17B).

Quadrate and mandible (Fig. 14A) as described for *A. monticola avia*.

Urohyal relatively narrow, typically widest about middle of length, or approaching tear-drop shape; anterior bifurcation moderately long, delicate (Fig. 15B); in large individuals urohyal may be long and very slender, as in *A. popoche* (Fig. 15A).

Rostral process of maxilla slopes sharply away from palatine process ventromesially, becoming more mesial in large specimens (> 140 mm),

but still remaining relatively short (Fig. 16A); articular facet on palatine process moderately to well developed; premaxillary process usually short; least depth of maxilla between ascending and palatine processes about one-half the distance between midpoints of these processes when stepped off along the curvature of the bone.

VARIATION.—Six nominal species have been described from various populations of *A. tincella*. Characters which seemed diagnostic to past investigators are eye length and interorbital distance as a proportion of head length, maximum body depth and head length as a percent of standard length, number of scales in the lateral line and between the lateral line and the origin of the pelvic fin, number of gill rakers, number of dorsal and anal fin rays, and the color of the body. We have carefully examined specimens from throughout the entire broad range of the species for these and other characters and find that at present we can justify only one name. We discern no taxonomically significant morphometric differences among any of the populations. Actually, in only one case is it possible to diagnose a species of *Algansea* on the basis of a morphometric character (*A. popoche*, see below), and here there are many other trenchant differences.

The number of scales between the insertion of the pelvic fin and the lateral line, a character utilized by Regan (1906-08), is much too variable to be useful when more than a few specimens are examined. This is true also of the color of the body, which varies according to age and environmental conditions. The remaining meristic characters show no variation between populations (number of dorsal and anal fin rays) or fall into the patterns described below.

Based on the number of gill rakers, there appear to be three semi-distinct groups of populations in *A. tincella*: those with high, low, and intermediate numbers (Table 3). The populations with the highest gill-raker numbers, from Lake Zacoalco and the Lake Chapala basin, are clearly associated with lakes or large rivers.

Populations with the least number of gill rakers are found in the region around Maravatío in the mid-Lerma basin, and in the Río Grande de Morelia and other tributaries of Lake Cuitzeo. These forms tend to live in moderate- to swift-flowing small streams.

The remaining populations with intermediate gill-raker numbers live in small streams of the Río Verde basin (near Valle de Guadalupe, TU 30704, and near Ojuelos, UMMZ 161663) and in the Río Ameca basin, or in large lakes (Sayula) and/or regions with pronounced lacustrine histories (Valley of Tocombo and Valley of México).

The few specimens from the Bajío (West, 1964:fig. 3; Barbour, 1973b) available to us suggest that some differentiation in gill-raker number may have occurred in this basin. The syntypes of the nominal species *A. dugesi*, one from Lake Yuriria (an artificial body of water dating from the 16th century) and the other from the city of Guana-

juato, have 20 and 21 rakers respectively. Other specimens from the ríos Turbio and Tigre have from 14 to 17. A clinal pattern of variation ranging from low numbers of rakers in tributaries to the Río Lerma to high numbers in the Río Lerma and other base-level localities is clouded by other individuals from Lake Yuriria with 14 to 16 gill rakers. Further studies of material from the Bajío region are clearly needed.

The number of median lateral scales (Table 1) shows the same basic pattern. Here, however, the populations from Lake Sayula and the Valley of Tocumbo have higher values and forms from the Río Grande de Morelia tend to fall within the intermediate group. Here also the pattern within the Bajío is not clear. Specimens from the ríos Turbio and Tigre and one individual from Lake Yuriria have 55 to 65 median lateral scales. The two syntypes of *A. dugesi* have at least 71 and 76 scales, the former taken from the lake.

The number of preoperculomandibular pores (Table 2) shows a slightly different pattern. Populations living in the region of the ancestral Chapala basin (interior basins and Lake Chapala and Tocumbo basins), except perhaps for those in Río Teuchitlán, tend to have higher values for this character. The increased number of pores in this sensory canal is probably correlated with the past lacustrine history of this region.

ECOLOGY.—*Algansea tincella* is ubiquitous in a variety of habitats ranging from small streams to lakes. We have, however, rarely seen the species in the nets of the commercial fishermen along the shore of Lake Chapala, although we have taken it in the Río Grande de Santiago at Poncitlán and in the Río Tizapán on the southern side of the lake. We judge that the species is probably less rare at the poorly collected eastern end of the lake near the mouth of the Río Lerma and near the origin of the Río Grande de Santiago.

Based on observations of gonad and tubercle development, spawning appears to occur from late May into July. The fact that specimens from the Río Tizapán were tuberculate suggests that the Lake Chapala population enters the tributaries to spawn.

MATERIAL EXAMINED.—Aguascalientes: UMMZ 189068(91), El Gigante Reservoir, near Santa María de Gallardo, 20.9 km NE hwy 45 on road to Loreto (at La Dichosa); TU 30676(14), Rodriguez Reservoir, 17.7 km W Aguascalientes, hwy 70. Federal District: FMNH 4529(8), Viga Canal. Guanajuato: UMMZ 189028(2), Río Tigre, just above Jerécuaro; UMMZ 189045(27), Lake Yuriria, along SW side, dredged channels; UMMZ 192318(4), trib. Río Turbio, 29.8 km NW Cuerámbaro; UMMZ 192414(2), Solís Reservoir, 6.4 km N Acámbaro; UMMZ 192518(1), Río Turbio about 12.9 km E Pénjamo at hwy 110 crossing; UMMZ 192563(1), Guanajuato; UMMZ 192564(1), Salamanca. Hidalgo: P 1942(3), Endhó Reservoir, Río Tula. Jalisco: UMMZ 108643(2), Río Grande de Santiago between Ocotlán and Lake Chapala; UMMZ 124458(5), Lake Chapala at Chapala; UMMZ 160905(2), 20.9 km S and 24.2 km W Guadalajara; UMMZ 161663(145), small stream 32.2 km SW Ojuelos; UMMZ 172121(1), roadside ditch about 12.9 km E Ameca; UMMZ 172196(4), trib. Río Verde at Cuarenta, about 24.2 km NE Lagos de Moreno; UMMZ 172220 (104, 2 cleared and stained), Río Teuchitlán, trib. Río Ameca at Teuchitlán; UMMZ 173545(2), trib. Río Ameca at La Vega, about 64.4 km W Guadalajara;

UMMZ 173550(6), reservoir at Hacienda San Sebastian, 1.6 km N Ezatlán; UMMZ 173556(1), Lake Colorado, several km E Ezatlán; UMMZ 173563(6), Lake Atotonilco at Villa Corona; UMMZ 173572(7) and 173579 (22, 3 cleared and stained), pond near Santa Cruz de las Flores, several km S Guadalajara; UMMZ 178319(173), Lake Santa Magdalena, just S Magdalena; UMMZ 178324(4), roadside ditch on hwy 70, 38.6 km W jct. with hwy 15; UMMZ 179697(7), lateral irrigation ditch off main E-W canal, 4.0 km N Ezatlán on road to Magdalena; UMMZ 179710(3), flooded edge of Lake Chapala about 1.6 km S Ocotlán; UMMZ 179734(6), Lake Chapala at Tuxcuca; UMMZ 179752(31, 4 skeletons), Río de Tizapán, Tizapán; UMMZ 179754(26), Río Ancho about 8.0 km N Yahualica, hwy 80 alternate; UMMZ 179758(3), Río de Aguascalientes at Belén del Refugio; UMMZ 184898(21, 1 cleared and stained), muddy canal along dike at Lake Magdalena, near Magdalena; UMMZ 189053(625), San Luis Gonzaga, 34.6 km E Aguascalientes on hwy 70; UMMZ 189058(42), 38.6 km E Aguascalientes on hwy 70; UMMZ 192173(22), irrigation ditch 1.6 km along road to Antonio Escobedo, 9.7 km E Ezatlán; UMMZ 192187(12), trib. Río Ameca just W Ameca on road to Mascota; UMMZ 192246(124), Lake Sayula, 7.6 km N Sayula; UMMZ 192301(10), Río Lerma about 0.8 km NW jct. hwy 90 and hwy 110; BMNH 1892.2.8. 91-4(4), syntypes of *A. stigamatura*, Río Grande de Santiago; BMNH 1900.9.29.145-7(3), Río Grande de Santiago; FMNH 3653, type of *A. rubescens*, Río Grande de Santiago at Ocotlán; FMNH 16529-16536(8), paratypes of *A. rubescens*, same as FMNH 3653; TU 30679(24), Río Encarnación about 3.2 km W Encarnación de Diaz; TU 30683(57), trib. Río Verde about 11.3 km W Lagos de Moreno, hwy 80; TU 30688(1), Río San Juan de los Lagos about 3.2 km E town of same name, behind Alcalá dam; TU 30692(917), reservoir about 3.2 km S San Julian; TU 30697(116), San Miguel reservoir, about 3.2 km S San Miguel el Alto; TU 30701(3), Río de San Miguel at El Paso de la Laja, hwy 80; TU 30704(71), trib. Río Verde at hwy 80 crossing, about 9.7 km NE Valle de Guadalupe; TU 30706(32), trib. Río Verde at hwy 80 crossing, about 3.2 km NE Valle de Guadalupe; TU 30709(74), Río San José de Gracia at Tule dam, about 11.3 km W Arandas; TU 30711(16), trib. Río Grande de Santiago at hwy 80 crossing, about 9.7 km NE Zapotlanejo; TU 30716(16), trib. Río Grande de Santiago at hwy 80 crossing E side of Zapotlanejo; TU 30751(33), Lake Zacoalco about 16.1 km S Acatlán de Juarez, around culverts; TU 30760(2), Lake Atotonilco about 0.4 km W Villa Corona; TU 31962(33), Río Grande de Santiago at Poncitlán; USNM 130931, Yijana. State of México: UMMZ 108624(2), E shore Lake Texcoco; UMMZ 192561(1), FMNH 3689(8), and USNM 55747(1), Lake Texcoco; UMMZ 192562(1), Chalco; FMNH 3683(9), Chalco; USNM 55746(1), Chalco, canals. Michoacán: UMMZ 167677(4), SE side Lake Chapala, 3.2 km E La Palma; UMMZ 173629(10), canal at Tarecuato (behind dam), SW Zamora; UMMZ 178582(37), Río Grande de Morelia near Santiago Undameo, about 6.4 km SE Cointzio Dam; UMMZ 188804(2), Cointzio Reservoir about 12.9 km SW Morelia; UMMZ 189276(6), Lake Chapala at road from Morelia to Guadalajara, 90.2 km W Zamora; UMMZ 189608(218), La Canal on E side Tocumbo; UMMZ 189617 (1 skeleton) and 191687 (2), Querendaro Canal, 8.4 km ENE Alvaro Obregon; UMMZ 192391(22), trib. Río Lerma, 6.9 km S Maravatio; UMMZ 192394(2), canal 6.0 km NE Alvaro Obregon; UMMZ 192405(1), canal 8.8 km NE Alvaro Obregon; UMMZ 192437(21), trib. flowing toward Los Reyes, 3.5 km S Tocumbo; UMMZ 192525(4), San Juanico Reservoir about 8.0 km NE Cotija; P 949(20), paratypes of *A. alvarezii*, Lake Fresno near Maravatio; P 962(2), paratypes of *A. alvarezii*, irrigation canal E Maravatio; TU 30723(1), trib. Río Lerma at NE end Tanhuato de Guerrero; TU 30822(2), Río de Morelia at Cointzio dam; TU 30836(2), Lake Cuitzeo; TU 30863(15), below San Juanico Dam, about 8.0 km SE Cotija; USNM 48211(2), Lake Cuitzeo; USNM 130904(3), Morelia. Querétaro: TU 31876(23) and USNM 55748(14), Río San Juan del Río at San Juan del Río. San Luis Potosí: UMMZ 170942(9), Santa María del Río; UMMZ 186285(239), Río Santa María del Río, about 4.8 km by road above town of same name; UMMZ 189024(249), Río Santa María del Río about 1.6 km S Villa de Reyes; UMMZ 189577(66, 5 skeletons), San Ysidro Reservoir, about 3.2 km SW Jesus María; SCB 65-18(157) and UMMZ 193665(6 cleared and stained), Río Santa María del Río at hwy 57 crossing. Zacatecas: UMMZ 161666(25), small impoundment, 1.2 km S Ojo Caliente; UMMZ 161667(57), reservoir 4.8 km S Guadalupe.

Algansea lacustris Steindachner

Fig. 8A

Algansea lacustris Steindachner, in Therese von Bayern and Steindachner, 1895:526, pl. 3, figs. 1a,b (original description; type-

locality: Lake Pátzcuaro, Michoacán). Jordan and Evermann, 1900: 3140 (after Steindachner). Meek, 1902:78 and 1904:47 (descriptions). Eigenmann, 1904:304 (listed). De Buen, 1941:345 (development), 1944:265-74, 293-96 (biology); 1946b:109 (synonymy, distribution). Alvarez, 1950:48 and 1970:59 (keys). Alvarez and Cortés, 1962:103 (synonymy).

Algansea tarascorum Steindachner, in Therese von Bayern and Steindachner, 1895:527, pl. 3, figs. 2a,b (original description; type-locality: Lake Pátzcuaro, Michoacán).

RANGE.—Known only from Lake Pátzcuaro, Michoacán.

DIAGNOSIS.—Barbels absent; gill rakers 18 to 23; radii absent or obsolete on anterior field of scales; median lateral scales 79 to 90 (modal number about 85); mouth upturned.

DESCRIPTION.—Number of median lateral scales, gill rakers, and total number of preoperculomandibular pores are given in Tables 1-3. Other counts follow. Predorsal scales: 34(2), 36(3), 37(4), 39(5), 40(1), 41(2), 42(1), 45(1); scale rows between origin of dorsal fin and lateral line: 17(1), 18(1), 19(2), 20(6), 21(2), 22(1), 23(1); scale rows between origin of pelvic fin and lateral line: 11(2), 12(2), 13(5), 16(1); scale rows around caudal peduncle above lateral line: 19(2), 20(1), 21(2), 22(2), 23(1), 24(1); scale rows around caudal peduncle below lateral line: 17(1), 18(3), 20(3), 21(1); dorsal fin rays: 8(31), 9(3); anal fin rays: 7(32), 8(1); pectoral fin rays: 13(1), 15(1), 16(3), 17(14), 18(9),

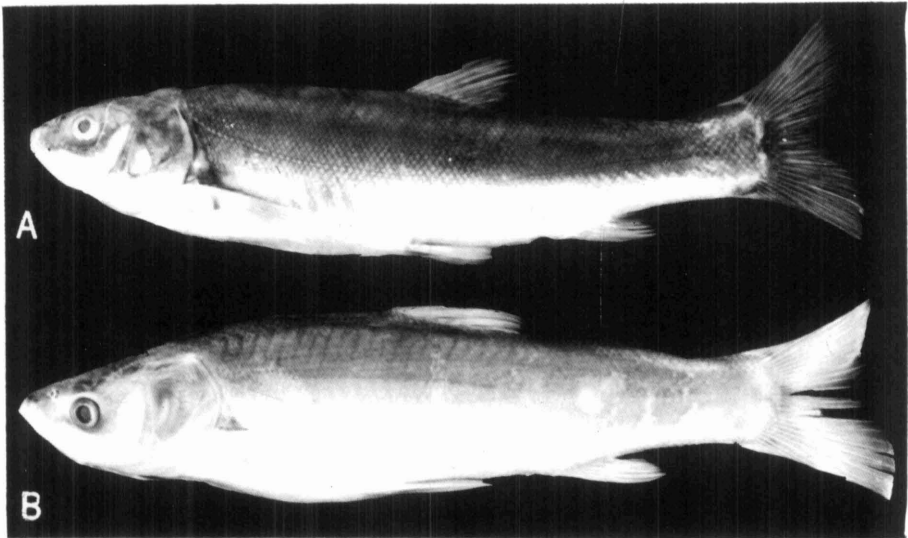


Fig. 8. Two species of *Algansea*: (A) *A. lacustris*, female, 165.5 mm, TU 30835; (B) *A. popoche*, male, 176.0 mm, UMMZ 192544.

19(3), 20(1); pelvic fin rays: 9(36), 10(3); supratemporal pores: 10(2), 11(1), 12(6), 13(7), 14(4), 15(3), 16(1); supraorbital pores: 11(1), 12(1), 13(8), 14(7), 15(2), 16(4), 17(1); infraorbital pores: 22(1), 24(2), 25(2), 26(8), 27(3), 28(3), 29(4), 30(1); preoperculomandibular pores: 17(1), 18(3), 19(3), 20(13), 21(8), 22(5), 23(1), 24(2); total vertebrae: 40(1), 41(9), 42(2).

Teeth 4-4; anterior part of dentigerous arch elongate, but ratio of anterior to posterior arm length less than 1.2.

Maximum length 263 mm (De Buen, 1941:347). A summary of proportional measurements for *A. lacustris* is presented in Table 5.

The pigmentation pattern is similar to that of *A. tincella* except that individuals tend to be darker dorsally, presumably because of the clarity of Lake Pátzcuaro. In life, adults are dark blue-green above and metallic silver below (De Buen, 1944).

The tubercle pattern is unknown.

Except for the infraorbital bones, which appear to have crenate margins (Fig. 17C), the osteology, based on two specimens about 80 mm, and the gut-coiling pattern, are the same as in *A. tincella*.

ECOLOGY.—Spawning takes place in the open waters of Lake Pátzcuaro from the end of November into May with peak activity occurring from February through April. The pelagic eggs drift towards shore where development and hatching occur in the warmer shallows (De Buen, 1944).

MATERIAL EXAMINED.—All from Lake Pátzcuaro, Michoacán: UMMZ 154343(12), 28 July 1947; UMMZ 189275(7), 20 August 1960; UMMZ 192560(2), FMNH 3630(10), and USNM 55765(2), 18-22 May 1901; P 2151(8) and UMMZ 194165(2 cleared and stained), 15 April 1959; TU 30835(2), 29 July 1963; USNM 131689(3), 1892 or 1904.

Alganssea popoche (Jordan and Snyder)

Fig. 8B

Xystrosus popoche Jordan and Snyder, 1900:123, fig. 5 (original description; type-locality: Lake Chapala, near Ocotlán, Jalisco). Jordan and Evermann, 1900:3142 (description). Meek, 1904:43, fig. 7 (synonymy, description). De Buen, 1946a:270-271 (synonymy, habits, description); 1946b:110 (listed). Alvarez, 1950:47 and 1970:66 (keys).

RANGE.—Known from Lake Chapala and its outlet, the Río Grande de Santiago above the falls at Juanacatlán. The species probably also occurs in the lower reaches of the Río Lerma, adjacent to Lake Chapala.

DIAGNOSIS.—Barbels absent; gill rakers 53 to 87, increasing with age (Fig. 20); scales with radii on lateral and posterior fields only; gut forms

counter-clockwise flexure with apex directed anteriorly (Fig. 3E); lips thin; mouth strongly upturned, mandible 10.2 to 12.0 percent of standard length; interorbital width 10.8 to 12.2.

Neurocranium (Fig. 10B) subrectangular in dorsal view, the roof flattened, narrower than in *A. tincella* (Fig. 10A). Preethmoids not ossified. Width of supraethmoid greater than length, mesial part of leading edge deeply indented, separating two laterally convex projections. Convex surface of dorsal part of epiotics extends mesially with decreasing prominence across epiotic-supraoccipital suture, ending lateral to low ridges which run parallel to base of supraoccipital crest; posteroventrally, the epiotic-supraoccipital suture enters an elongate depression before meeting the exoccipital suture. Prominent eave-like arches project posteriorly from the epiotics; lateral wings of exoccipitals well developed, broad along their entire length. Roof of posterior myodome elevated, clearly visible through foramen magnum. Pharyngeal process of basioccipital delicate, perforated with foramina; ventral masticatory surface shaped as an elongate pentagon. Dentary elongate, slender (Fig. 14B). Maxilla slender, least depth between ascending and palatine processes goes three or more times into the distance between these processes when stepped off along the bone.

DESCRIPTION.—Number of median lateral scales, gill rakers, and preoperculomandibular pores are given in Tables 1-2 and Figure 20. Other counts follow. Predorsal scales: 22(1), 23(3), 24(5), 25(2), 26(4), 27(5), 28(4), 29(1), 30(1), 31(1); scale rows between origin of dorsal fin and lateral line: 12(1), 13(3), 14(4), 15(5), 16(4), 17(3), 18(1); scale rows between origin of pelvic fin and lateral line: 5(1), 7(3), 8(14), 9(10); scale rows around caudal peduncle above lateral line: 16(8), 17(3), 18(6); scale rows around caudal peduncle below lateral line: 13(3), 14(1), 15(3), 16(8), 17(2); dorsal fin rays: 8(26), 9(4); anal fin rays: 7(25), 8(5); pectoral fin rays: 16(1), 17(13), 18(15), 19(1); pelvic fin rays: 9(19), 10(11); supratemporal pores: 8(3), 9(3), 10(8), 11(10), 12(5); supraorbital pores: 10(1), 11(5), 12(11), 13(9), 14(1), 15(2); infraorbital pores: 19(1), 20(2), 21(1), 22(2), 23(4), 24(4), 25(6), 26(4), 27(2), 28(2), 29(1); preoperculomandibular pores: 16(2), 17(2), 18(6), 19(10), 20(4), 21(3), 22(1), 23(1); total vertebrae: 39(22), 40(15).

Teeth 4-4, slender; anterior arm of pharyngeal arch thin and elongate (Figs. 18C, 19C); ratio of anterior to posterior arm length greater than 1.2.

Maximum standard length about 230 mm. Proportional measurements are presented in Table 5.

Pigmentation as in *A. tincella*: light brownish gray dorsally, silvery white ventrally; lateral stripe very faint or absent.

Small, fleshy, recurved or blunt nuptial tubercles present on the pectoral and pelvic fins; arranged in two or more rows along the rays of the

pectoral fin with more than one tubercle per ray segment; present on the outer one-half of ray 2 and the outer three-fourths of rays 3 to 10. The files may branch twice. On pelvic fin, tubercles very weakly developed near the bases of rays 2 to 5. Tubercles distributed on head as in *A. tincella*; none found on body or on dorsal, anal, or caudal fins.

Butterfly-shaped supraethmoid projects forward from anterior margins of frontals (Fig. 10B), horizontal or tilted slightly upward in sagittal view, convex in cross section. Anterior margins of frontals truncate along sutures with supraethmoid and lateral ethmoids. Supraorbital margins usually weakly concave; postorbital projections of frontals not prominent; shelves lateral to anterior part of lateral temporal fossae narrow. Parietals excluded from contact with sphenotics by frontal-pterotic sutures. Deep recesses beneath epiotic arches connect laterally with the posttemporal fossae (Fig. 12B). Lateral wings of exoccipitals broad, as in *A. monticola avia* (unlike *A. tincella*), but with lateroventral margins slightly developed into posteriorly directed flanges. Lateral occipital foramina prominent, opening laterally more than posteriorly. Pharyngeal process of basioccipital descends obliquely from skull, not recurved to parallel vertebral column (Fig. 13B); pentagonal masticatory surface concave, lateral corners directed ventrally, about one-half to one-third of surface lies beneath skull; pharyngeal process relatively short, slender posteriorly, flattened distally to form a narrow, vertical paddle.

Infraorbital bones enlarged as in *A. tincella* (Fig. 17B).

Mandible elongate (Fig. 15B); biting edge of gnathic ramus weakly deflected laterally and slightly enlarged at symphysis.

Urohyal long and very slender, anterior bifurcation long and delicate (Fig. 15A).

Rostral process of maxilla elongate, sloping gently away from palatine process in mesial and slightly ventral direction; articular facet on palatine process not well developed in specimens examined; premaxillary process very short (Fig. 16C).

VARIATION.—The differences between the total number of gill rakers in specimens of *A. popoche* from the Río Grande de Santiago at Poncitlán (TU 31963) and Lake Chapala (UMMZ 167717), shown by the two clusters in Figure 20, appears to be a function of age. The values for Poncitlán (53-70) were obtained from specimens ranging in length from 49 to 82 mm ($\bar{X} = 60.9$ mm). Within this size range the number of gill rakers is positively correlated with length ($P < .01$). The higher counts from Lake Chapala (67-87) were taken from specimens ranging in length from 84 to 178 mm ($\bar{X} = 97.5$ mm). Within this size range there is no significant correlation between the number of gill rakers and length ($P > .05$). We do not exclude the possibility that *A. popoche* from a fluvial environment may have a lower modal number of gill rakers or that possibly introgression (see below) has influenced gill-raker number, but we cannot test these hypotheses with our data.

TABLE 6
COMPARISON OF SELECTED CHARACTERS OF *A. POPOCHE*, HYBRIDS, AND *A. TINCELLA*
MEASUREMENTS IN MILLIMETERS; MEANS IN PARENTHESES

Locality	Hybrids			<i>A. tincella</i> ² Rio de Tizapán 65.9-99.8 (89.0)
	<i>A. popoche</i> ¹ Lake Chapala 83.9-98.5 (92.8)	Poncitlán ³ 91.5	L. Chapala ⁴ 90.9	
Standard length				
Head length	28.2-31.2 (29.8)	27.2	30.5	23.7-26.4 (25.4)
Postorbital head length	15.0-18.0 (16.6)	14.4	17.6	13.2-15.4 (14.3)
Snout length	8.1-9.3 (8.7)	7.2	8.7	6.7-7.8 (7.2)
Upper jaw length	7.7-9.2 (8.2)	7.2	7.6	6.0-7.0 (6.4)
Mandible length	10.3-12.0 (11.0)	9.8	11.1	7.5-9.1 (8.3)
Caudal peduncle length	21.6-25.1 (23.0)	22.7	22.3	19.4-22.8 (21.2)
Least depth	10.6-11.9 (11.4)	12.5	11.8	11.9-14.2 (12.9)
Pelvic fin length	14.8-16.5 (15.8)	16.5	16.8	12.9-15.7 (14.6)
Gill rakers	64.0-84.0 (73.3)	33.0	53.0	17.0-23.0 (21.1)
Preoperculo-mandibular pores	36.0-45.0 (38.4)	34.0	37.0	25.0-36.0 (31.0)
Scale radii	Lateral and posterior fields	All fields	Lateral and posterior fields	All fields
Curvature of gut	Fig. 3E	Fig. 3E	Fig. 3E	Fig. 3C,D

¹Based on UMMZ 167717 (24 specimens).

²Taken from Rio de Tizapán, a small southern tributary to Lake Chapala east of Tizapán. The collection station is less than 1 km from the lake. Based on UMMZ 179712 (18 specimens).

³A town on Rio Grande de Santiago north of Lake Chapala; TU 82781.

⁴Based on UMMZ 193676.

HYBRIDIZATION.—In the course of our study, a number of specimens of *Algansea* were noted whose total number of gill rakers falls between the values for *A. tincella* and *A. popoche* (Fig. 20). These individuals were taken from Lake Chapala and its outlet, the Río Grande de Santiago. One of the specimens is a paratype of the nominal *A. rubescens* (FMNH 16531), 105 mm SL, with 32 rakers. Three specimens whose lengths are within the size ranges of our series of presumed parental species are compared in Table 6. Unfortunately, for purposes of comparison, we do not have adequate series of *A. tincella* from either hybrid locality or of *A. popoche* from Poncitlán (our station on the Río Grande de Santiago). Both species occur at both localities, however.

Besides the number of gill rakers (Fig. 20), intermediacy was noted in the shape of the pharyngeal arch and strength of the teeth (Figs. 18 and 19). The total number of preoperculomandibular pores also falls between 34 and 38, close to the value (36) at which both species overlap. On the basis of these characteristics, we consider the specimens to be hybrids between *A. tincella* and *A. popoche*. Of the 24 morphometric conditions (Table 6, eight characters, three specimens), nine are more or less intermediate, 12 resemble *A. popoche*, and three are closer to *A. tincella*. In the curvature of the gut and the degree to which radii are present on the scales, the hybrids also more closely resemble *A. popoche*.

There are three possible explanations why so many of the morphometric character states of the hybrids fall within the range of one or the other parental species. The first is that the specimens are not hybrids. We reject this on the basis of intermediacy in the number of gill rakers and the characteristics of the mandibular arch and pharyngeal teeth. Second, most of the characters listed in Table 6 are almost certainly controlled by multiple genes. Among F_1 individuals, for any particular character, there will be a frequency distribution which, if the difference between the parental ranges is slight, will most likely overlap the parental values to a greater or lesser extent. To test for intermediacy, the character states of the individual parents would have to be known. Finally, the presence of dominant genes in a multiple gene system may result in the frequency distribution of an F_1 or F_2 character state being strongly skewed toward that of one of the parents. The most extreme situation is the coupling of dominance with genes having additive or subtractive effects (Grant, 1975, multiple gene systems, oppositional model). In this case F_1 phenotypes may result whose values exceed those of the parents (transgressive segregation).

We make these comments not to justify ambiguous data, but to suggest that, theoretically, the lack of intermediacy does not necessarily preclude the presence of a hybrid (Clark Hubbs, 1956). Controlled breeding experiments are, of course, the only way to solve this problem unequivocally.

The occurrence of the hybrids may be explained on the basis of overlap in the time and place of spawning of *A. popoche* and *A. tincella*. It is also noteworthy that the specimens taken at Poncitlán were collected in the sluiceways below a dam across the Río Grande de Santiago. Hybridization below artificial barriers across streams and rivers is fairly common in fishes (Raney, 1940).

ECOLOGY.—According to Cuesta Terrón as cited by De Buen (1946a), *A. popoche* occurs throughout Lake Chapala but is more common at the mouths of rivers and streams in areas where there is aquatic vegetation. Spawning coincides with the rainy season and takes place in the streams and rivers of the Lake Chapala basin between the middle of June and the end of August.

De Buen (1946a) also stated that Cuesta Terrón found mud and remains of vegetation in the stomach of *A. popoche*, indicating that the species probably feeds by ingesting mud and organic matter, filtering out the food particles with its long, slender gill rakers. Of the 19 or 20 fish species with which it coexists, it is the only one that appears to utilize this particular food source as an adult.

Algansea popoche was probably much more abundant prior to 1909-1912. At that time a dike was constructed across part of Lake Chapala near the Lerma delta to reclaim almost 50,000 hectares of swamp. This project destroyed a large part of the standing vegetation of the lake (Goldman, 1951) that must have been prime habitat for this species.

MATERIAL EXAMINED.—Jalisco: UMMZ 108633(4), Río Grande de Santiago between Ocotlán and Lake Chapala, 10 December 1932; UMMZ 167717(49, 2 cleared and stained), NW side Lake Chapala, 10 July 1949; UMMZ 179704(4 skeletons), Lake Chapala at SW end, opposite Ajijic, 9 March 1961; UMMZ 179711(2), flooded edge of Lake Chapala about 1.6 km S Ocotlán, near source of Río Grande de Santiago, 10 March 1961; UMMZ 179735(1), Lake Chapala at Tuxcueca, 13 March 1961; UMMZ 192544(1), Lake Chapala, 6.1 km W Ajijic, 21 June 1969; CAS-SU 6151, type, Lake Chapala, Ocotlán, 26 December 1898; TU 31963(43, 12 cleared and stained), Río Grande de Santiago at Poncitlán, 1 April 1964. Michoacán: UMMZ 179726(1 skeleton), Lake Chapala at La Palma, 12 March 1961.

ANALYSIS OF CHARACTER STATES

Our phylogenetic analysis of *Algansea* is based, in part, upon the method of Hennig (1966). Two species or groups of species sharing derived character states are assumed to have evolved from an immediate common ancestor (if convergence has not occurred) and are considered to be more closely related to each other than to taxa lacking the character states. We attempted to determine the evolutionary direction of the transformation states of any given character (Maslin, 1952) by using the criteria of Kluge and Farris (1969). A character state is considered primitive for a particular group if it is (in order of reliability) (1) widely

TABLE 7
 MATRIX OF CHARACTER-STATE CODE VALUES FOR THE SPECIES OF *ALGANSEA* AND
 COORDINATE-BY-CHARACTER LOADINGS FOR EACH CHARACTER ON THE FIRST FIVE PRINCIPAL AXES

Number	Character	Principal Coordinate										
		<i>A. aphanea</i>	<i>A. monticola</i>	<i>A. barbata</i>	<i>A. tinella</i>	<i>A. lacustris</i>	<i>A. popoche</i>	I	II	III	IV	V
1	Length	0	0	-1	0	1	1	-	.6	-	-	-
2	Mouth	-1	0	-1	0	1	1	.4	-	-	-	-
3	Eyes	-1	0	0	0	0	0	.5	-.3	-	-	-
4	Barbels	1	1	1	0	0	0	-1.0	-.6	-.4	-	-
5	PM pores	0	0	0	1	1	1	.4	-	-	-	-
6	Scale radii	0	0	0	0	0	1	-	-.4	-	-	-.3
7	Gill rakers	0	0	0	1	1	1	.4	-	-	-	-
8	Gut flexure	0	0	-1	1	1	1	.3	-.4	-	-	-
9	Skull outline	0	0	0	0	0	0	-	.4	-	-	-
10	Epiotic arches	-1	0	0	0	1	1	.5	-	-	-	-
11	Supraethmoid margin	-1	0	0	1	1	1	.5	-	-	-	-
12	Dentary flexure	1	0	0	0	0	0	-1.1	-	-	-	-
13	Dentary strength	0	0	0	0	0	0	-	.4	-	-	-
14	Dermosphenotic	1	0	0	0	0	0	-1.1	-	-	-	-
15	Frontal	0	0	1	0	0	0	-.5	-.5	-.8	.3	-
16	Parietal	1	0	0	0	0	0	-1.1	-	-	-	-
17	Basioccipital	0	0	0	0	0	0	-	.4	-	-	-
18	Spawning location	0	0	0	0	0	1	-	-.8	.5	-	-
19	Lateral scales	0	0	0	0	0	1	-	-.8	.5	-	-
20	Ventral urohyal	0	1	1	1	1	1	.5	-	-.3	-	-
21	Anterior urohyal	0	1	1	1	1	1	.4	-.6	-.4	-	-
22	Supraethmoid orient.	0	1	1	1	1	1	.5	-	-.3	-	-
23	Skull dome	0	0	1	1	1	1	.4	-	-.4	-	-.4
24	Maxilla I	0	0	0	0	0	0	-	.4	-	-	-
25	Maxilla II	1	0	0	0	0	0	-1.1	-	-	-	-
26	Pharyngeal arch	0	0	0	0	0	0	-	.4	-	-	-

distributed in many representatives of closely related groups, (2) widely distributed within the group, and (3) associated with other character states known from other evidence to the primitive.

A detailed study of North American Cyprinidae to determine the status of the character states present in *Algansea* is beyond the scope of this paper. Although we surveyed other cyprinid genera (see MATERIALS AND METHODS) we reasoned that the closest relatives of *Algansea* would most likely be found in northern México or in southwestern United States. For this reason we centered our attention on the genus *Gila*.

Of the list of characters presented below, the first 18 represent those for which we feel reasonably confident that we have determined primitive and derived states. Evolutionary sequences were not determined for the remaining eight characters; they were added to the set for the phenetic analysis only. All character states are summarized in Table 7.

The appearance of a negative number in our phylogeny (Fig. 23) is the result of our using a coding system compatible with both phenetic and phylogenetic analyses. In our scheme we have arbitrarily used the number 0 to designate primitive states and, in most of the characters, the numbers 1 and 2 indicate both the form and the sequence of the morphoclines. In characters 1-3, 8, 10, and 11, however, the primitive states are located within the morphoclines. In character 2, for example, coding the character states 0, 1, 2, 3 preserves the direction of the trend but not the form. This is permissible in phyletics because the numbers are only serving as labels, i.e., a nominal scale is used. In a phenetic analysis, however, an ordinal scale is required, one that preserves the form of the morphocline. Hence we have had to incorporate a -1 into the character state coding of these six characters.

As noted by Smith and Koehn (1971), the coding of the character states affects the results of any study such as ours. The lack of a method to account for variation forced us to recognize mean values as states of continuous variables. For discrete variables (e.g., osteological characters) it was necessary to code the "typical" condition and overlook the variants that appear to link species pairs. Both difficulties would have been greatly reduced in our phenetic analysis if raw data had been used. Unfortunately, it is not always possible to obtain information on the external and internal anatomy of the same specimens and still have sample sizes large enough to estimate accurately the range of variation. Also, interpretational difficulties arise if coded and raw data are mixed unless the former reflect a logical sequence. Other sources of error are our occasional use of compound characters and the possible recognition of differences based on size. Because of the latter difficulty or lack of knowledge concerning the range of variation, many possibly useful characteristics (e.g., the suspensorium of *A. aphanea* and the morphology of the articular) were not used. Clearly, more

specimens and the use of individuals as OTU's would have resulted in an analysis with much greater resolving power.

1. STANDARD LENGTH.—*A. aphanea* and *A. monticola* are small species reaching a maximum length of about 85 to 95 mm. *A. barbata* attains a length of about 130 mm. Most populations of *A. tincella* range from 60 to 100 mm although we have seen individuals as large as 174 mm (FMNH 3683). As the great majority of our specimens fall within the 60 to 100 mm size range, we have assigned *A. tincella* to character state 0. Maximum lengths of *A. lacustris* and *A. popoche* are in the vicinity of 263 and 230 mm, respectively. We recognize three states of character 1 and consider the smaller lengths to be primitive (Smith et al., 1975).

- 1 = maximum length about 130 mm
- 0 = maximum length between 85 and 100 mm
- 1 = maximum length between 230 and 263 mm

2. ORIENTATION OF MOUTH.—All species of *Gila* have a variably terminal mouth. We consider this condition to be primitive. Because *A. lacustris* and *A. popoche* differ in the degree of obliquity of their mouths, we recognize four states of character 2.

- 1 = subterminal
- 0 = terminal
- 1 = upturned
- 2 = strongly upturned

3. ORIENTATION OF EYES.—All species of *Gila* have lateral eyes. We consider this condition to be primitive and recognize three character states in *Algansea*.

- 1 = slightly upturned
- 0 = lateral
- 1 = slightly downturned

4. BARBELS.—Barbels are not present in the genus *Gila* and are lacking in *A. tincella*, *A. lacustris*, and *A. popoche*. We consider barbels to be derived in *Algansea* and recognize two character states.

- 0 = absent
- 1 = present

5. CEPHALIC LATERAL-LINE SYSTEM.—The only head pore canal in *Algansea* in which there is significant interspecific variation is the preoperculomandibular system (Table 2). Most of the genera of North American cyprinids, including *Gila*, have preoperculomandibular counts that broadly overlap those of *A. aphanea* and *A. monticola* or are lower (Illick, 1956), and for this reason these two species are considered to be primitive for this character. We recognize three overlapping states of character 5. (Because of the small sample size, we have not used counts of *A. barbata* in calculating means and have arbitrarily assigned it to state 1.)

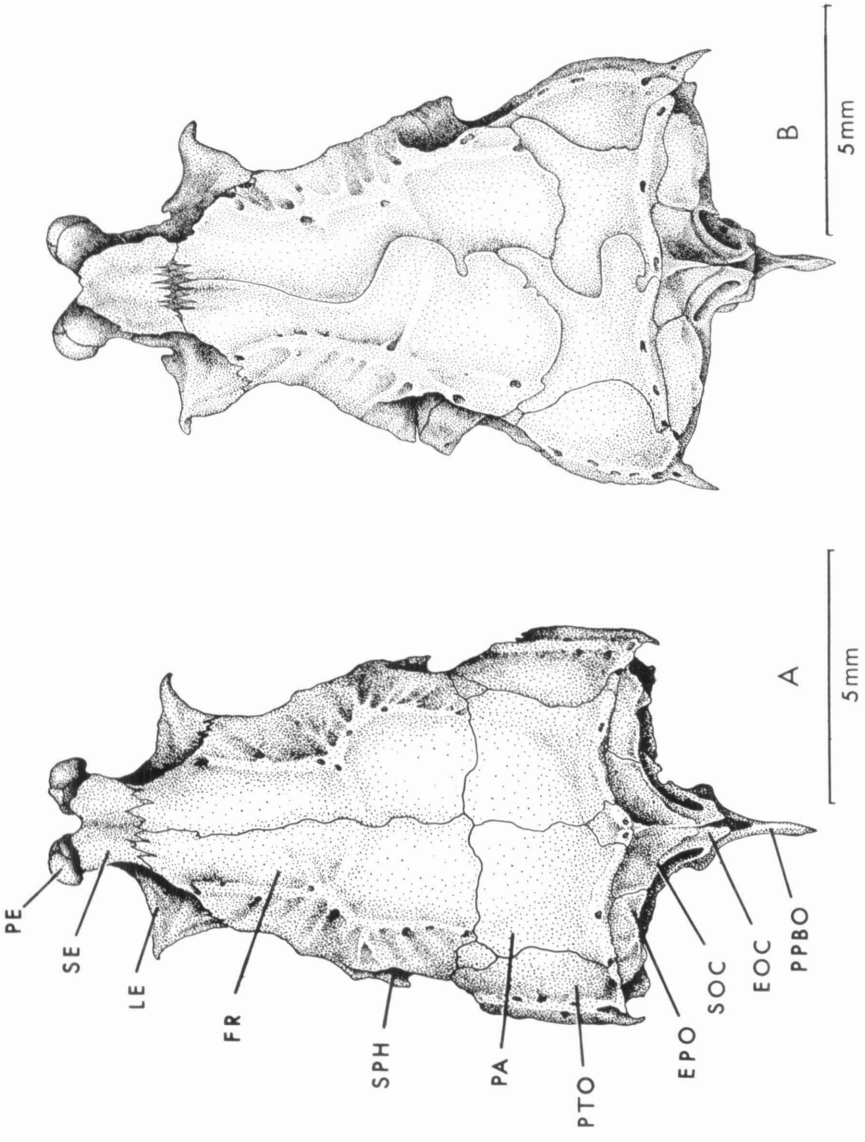


Fig. 9. Dorsal view of neurocrania of two species of *Alganssea*: (A) *Alganssea monticola avia*, 59.1 mm, UMMZ 192188; (B) *Alganssea aphanea*, 82.0 mm, UMMZ 192196. For abbreviations see text (MATERIALS AND METHODS).

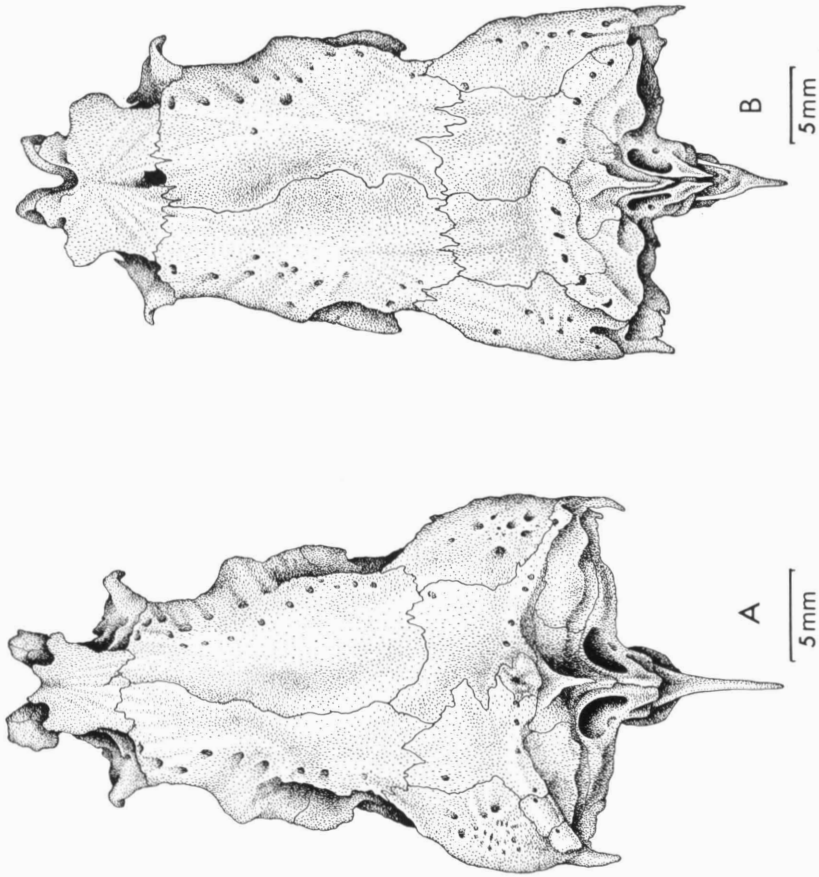


Fig. 10. Dorsal view of neurocrania of two species of *Algansea*: (A) *Algansea tinella*, 175 mm, UMMZ 189577-S; (B) *Algansea popoche*, 180 mm, UMMZ 179704-S.

0 = 17-28 (\bar{X} = 21.3)

1 = 20-39 (\bar{X} = 28.3)

2 = 34-48 (\bar{X} = 39.3)

6. SCALE RADII.—The degree to which radii are present on the scale fields is variable within *Gila* (e.g., Miller, 1945). Within *Algansea* and the subgenus *Temeculina*, however, all species except two have radii on all scale fields. Radii are lacking or obsolete on the anterior fields of *A. lacustris* and *A. popoche*, two species adapted to a lacustrine environment. We recognize two states of character 6.

0 = present on all scale fields

1 = reduced or lacking on anterior scale field

7. GILL RAKERS.—High numbers of gill rakers are associated with filter-feeding inhabitants of lakes and rivers. As these species are usually derived from fluvial forms with low numbers of gill rakers, the former is considered a derived and the latter a primitive character state. The number of gill rakers varies widely in *Gila*, particularly among those populations isolated as Great Basin relicts. Counts for *G. bicolor* range from 8 to 40 (Hubbs et al., 1974). In the subgenus *Temeculina*, the number is low, falling within the range found in *A. aphanea*, *A. monticola*, and *A. barbata* (Table 3). We recognize three states of character 7.

0 = 5-11 (\bar{X} = 7.5)

1 = 9-25 (\bar{X} = 15.5)

2 = 49-84 (\bar{X} = 66.4)

8. FLEXURE OF GUT.—All species of *Gila* have a gut flexed in a simple loop as in *A. monticola avia*, *A. aphanea*, and most specimens of *A. monticola monticola*. We consider this arrangement to be primitive and recognize four states of character 8 in *Algansea* (Fig. 3).

-1 = simple loop with median part flexed sharply to the right

0 = simple loop

1 = counter-clockwise flexure directed posteriorly or laterally across the ventral side of the body cavity to the left

2 = counter-clockwise flexure directed anteriorly

9. DORSAL OUTLINE OF NEUROCRANIUM.—The dorsal outline of the neurocranium varies in *Algansea* from triangular-subtriangular (Fig. 9) with broad, concave supraorbital margins (in *A. aphanea*, Fig. 9B) to rectangular (Fig. 10B). However, it is difficult to tell which is the primitive and which is the derived state. The first two characteristics are pronounced not only in *A. aphanea* but also in the subgenus *Temeculina* of *Gila*, *Richardsonius*, *Clinostomus*, *Mylopharodon*, *Acrocheilus*, *Pogonichthys*, *Ortiodon*, *Phoxinus*, some *Hybopsis*, *Pimephales*, and *Campostoma*. On the other hand, neurocrania with straight margins are found in *Semotilus*, *Hybognathus*, *Rhinichthys*, and some *Notropis* (G. R. Smith, pers. comm.). The rectangular neurocranium

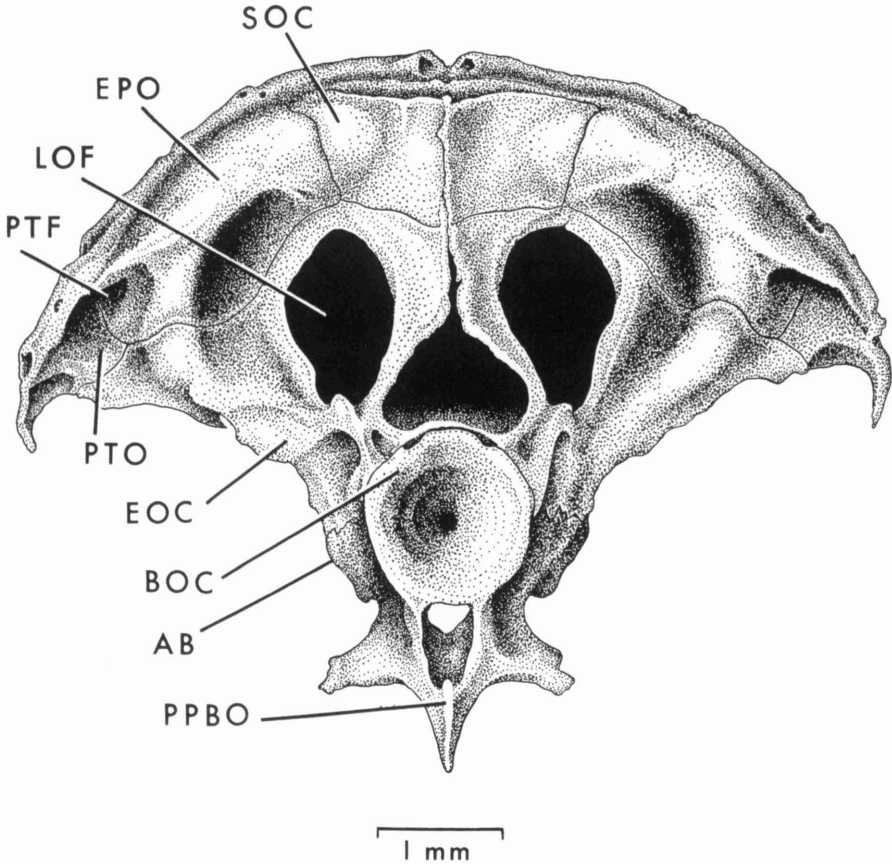


Fig. 11. Posterior view of neurocranium of *Algansea monticola avia*, 59.1 mm, UMMZ 192188. For abbreviations see text (MATERIALS AND METHODS).

of *A. popoche* is unique in *Algansea*. In the species of *Gila* examined, it occurs only in *G. cypha*, *G. elegans*, and *G. robusta*, specialized forms adapted for living in large, swift rivers. For these reasons we consider a rectangular neurocranium to be derived and recognize two states of character 9.

- 0 = triangular-subtriangular in dorsal outline
- 1 = rectangular in dorsal outline

10. CONFIGURATION OF POSTERIOR FACE OF NEUROCRANIUM: SCULPTURING ON EPIOTIC BONES.—Posterior projections of the epiotics of varying degrees of prominence serving as points of attachments for epaxial muscles were found in all species of cyprinids examined except *Notropis chalybaeus* (Cope). Most common configurations were arch-like projections extending laterally across the epiotics, a single protuberance which may be spine-like, or a combination of these. In *Algansea*, arches

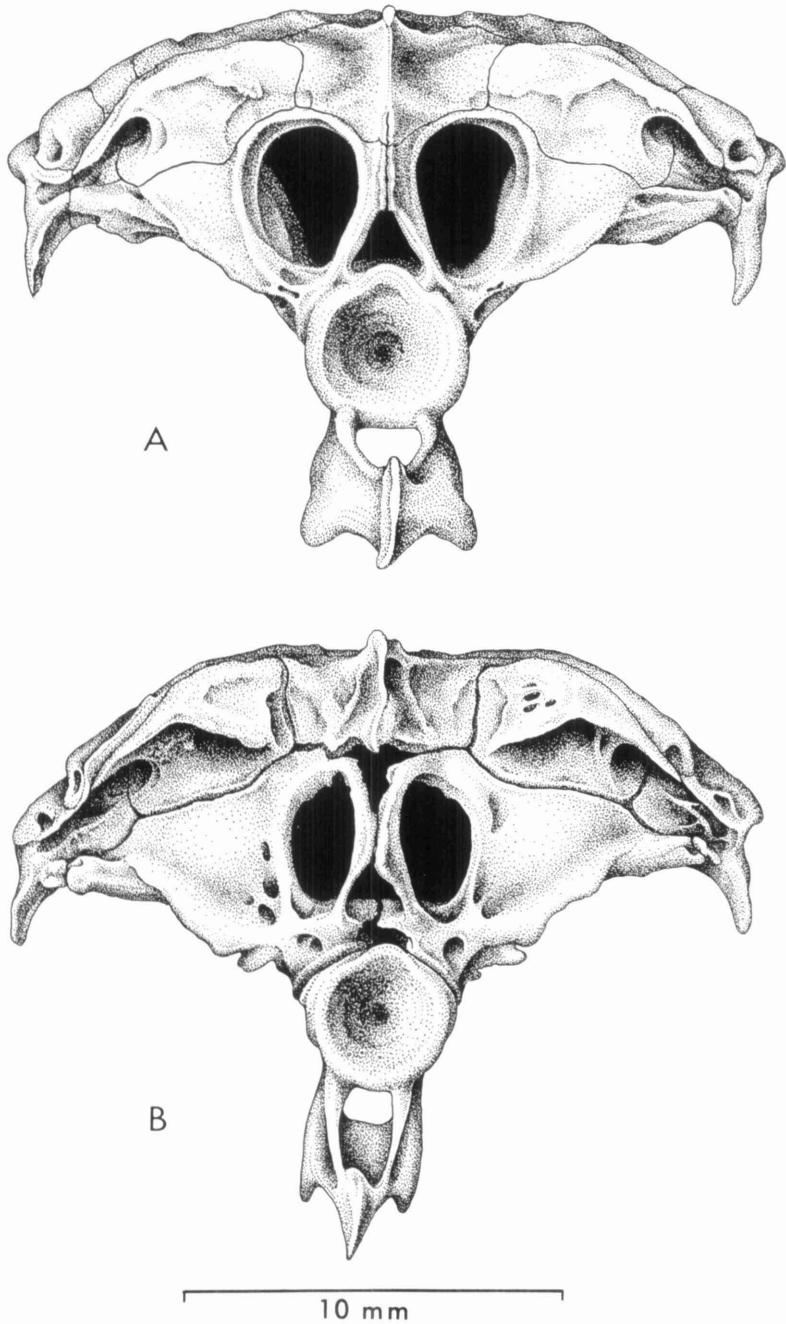


Fig. 12. Posterior view of neurocrania of two species of *Algansea*: (A) *Algansea tincella*, 175 mm, UMMZ 189577-S; (B) *Algansea popoche*, 180 mm, UMMZ 179704-S. The displacement of the basiocipital of *A. popoche* was the result of having to reconstruct the posterior part of the skull.

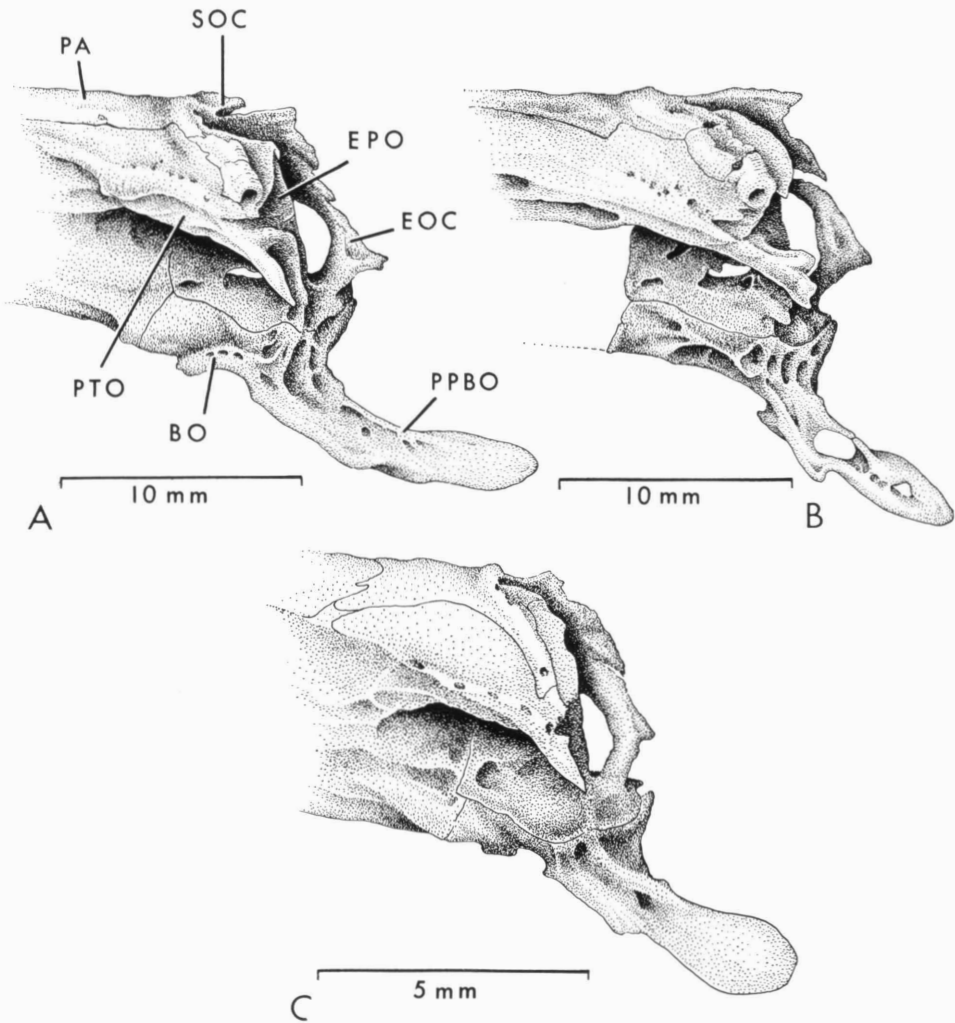


Fig. 13. Lateral view of posterior part of neurocrania of three species of *Algansea*: (A) *A. tincella*, 175 mm, UMMZ 189577-S; (B) *A. popoche*, 180 mm, UMMZ 179704-S; (C) *A. aphaenea*, 82 mm, UMMZ 192196. For abbreviations see text (MATERIALS AND METHODS).

were present as a morphocline: absent or very weakly developed in *A. aphaenea*, weakly developed in *A. monticola* and *A. barbata*, prominent in *A. tincella* and *A. lacustris*, and very strongly developed in *A. popoche* (Figs. 11, 12, 13). The condition found in *A. popoche* appears to be associated with the lacustrine habits of that species and is thus considered a derived state. We recognize four states of character 10.

- 1 = absent or obsolete
- 0 = weakly developed
- 1 = prominent
- 2 = very strongly developed

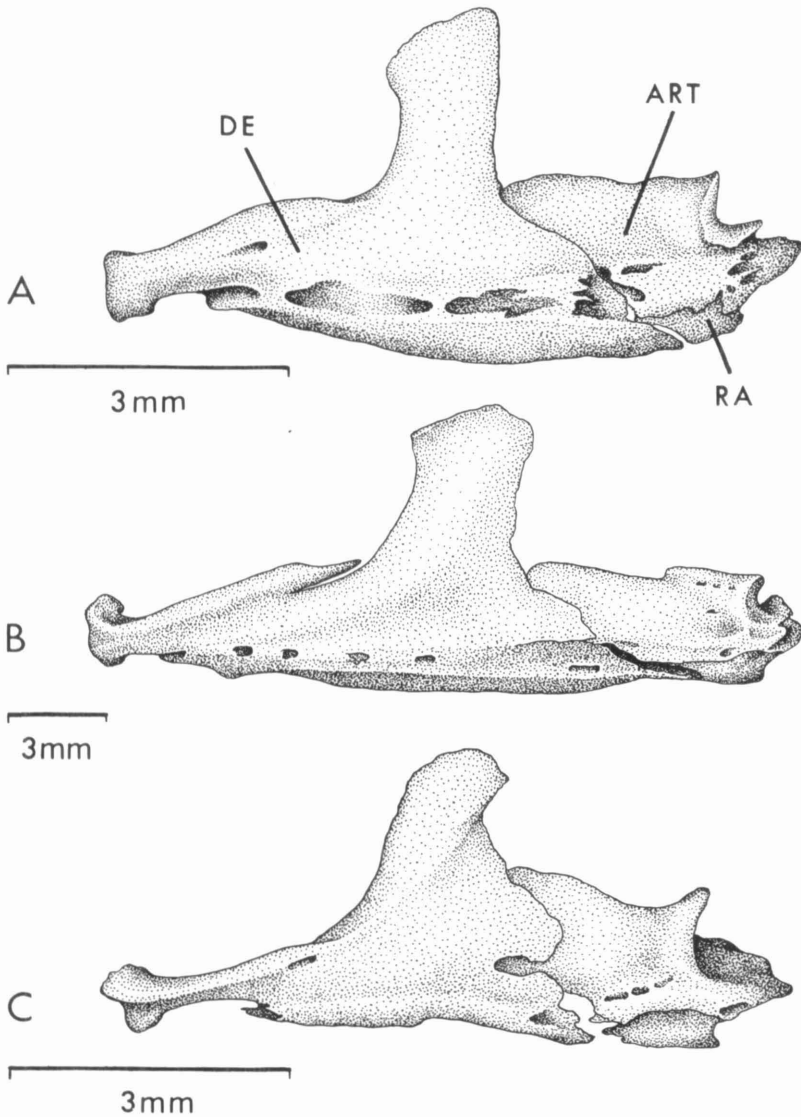


Fig. 14. Lateral view of mandibles of three species of *Algansea*: (A) *A. tincella*, 86.1 mm, TU 30704; (B) *A. popoche*, 180 mm, UMMZ 179704-S; (C) *A. aphaea*, 76.5 mm, UMMZ 192196. For abbreviations see text (MATERIALS AND METHODS).

11. ANTERIOR MARGIN OF SUPRAETHMOID BONE.—A moderately broad supraethmoid with a single anterior U-shaped notch is found in most species of *Gila*, although the overall shape of the bone tends to be

variable even within species (Uyeno, 1961). We recognize four states of character 11 in *Algansea* (Figs. 9, 10).

-1 = rounded, median U-shaped notch absent

0 = single U-shaped notch

1 = 3 U-shaped notches

2 = 3 U-shaped notches, the middle indentation the deepest

12. GNATHIC RAMUS OF DENTARY: FLEXURE.—The biting edge of the gnathic rami of *Gila* and all but one species of *Algansea* is vertical or very nearly so. In *A. aphanea* it is deflected sharply to the side (Fig. 14C). We consider this to be a specialized condition and recognize two states of character 12 in *Algansea*.

0 = biting edge vertical or nearly so

1 = biting edge deflected laterally

13. GNATHIC RAMUS OF DENTARY: STRENGTH.—The shape of the anterior part of the dentary is variable in *Gila* and is most likely related to the feeding habits of the individual species. In the subgenus *Temeculina*, it is moderately robust. The gnathic ramus of *A. popoche* is long and delicate, an obvious specilization associated with its filter-feeding habits. As it is not possible to determine the primitive state from among the remaining variants (e.g., moderately robust, robust), we have recognized only two states of character 13 in *Algansea* (Fig. 14).

0 = robust or moderately so

1 = attenuate, delicate

14. DERMOSPHENOTIC BONES.—Although plate-like dermosphenotics represent a derived character state when viewed in the context of the North American Cyprinidae, the character state is primitive in the context of the species of *Algansea*. *Algansea aphanea* is the only member of the genus with a tubular dermosphenotic (Fig. 17). We consider this to be a character reversal and thus derived and recognize two states of character 14 in *Algansea*.

0 = plate-like

1 = tubular

15. FRONTAL BONES.—In *A. barbata* blunt, posterolateral projections from the frontals form wide shelves lateral to the anterior part of the lateral temporal fossae. This condition is unique in *Algansea* and *Gila* and is considered derived. We recognize two states of character 15.

0 = do not project laterally beyond sphenotics

1 = project laterally beyond sphenotics

16. PARIETAL BONES.—Among the species of *Gila*, the parietals are rectangular. In *Richardsonius balteatus* and *Clinostomus elongatus* the parietals meet the sphenotics on the dorsal surface of the neurocranium (Uyeno, 1961, and our observations). This character state is also found in *A. aphanea* (Fig. 9B). We consider finger-like projections of the parietals to be derived, but not indicative of a close relationship to

Richardsonius and *Clinostomus* (i.e., a convergence) and recognize two states of character 16 (see also Description of *A. monticola avia*).

0 = finger-like projections absent

1 = finger-like projections present

17. BASIOCCIPITAL BONE.—As might be expected in a species which feeds on small particles, the pharyngeal process of the basioccipital in *A. popoche* (Fig. 13B) is narrower and more delicate than in those forms that feed on larger items. In the specimens we observed, the structure was also perforated by fenestrae and the grinding surface was smaller. On the basis of this trophic specialization, we recognize two states of character 17.

0 = pharyngeal process strong, robust or moderately so

1 = pharyngeal process narrow, delicate

18. SPAWNING HABIT.—As stated above (*A. popoche*: Hybridization, Ecology) *A. popoche* and, by inference, *A. tincella*, spawn in a fluvial environment. *A. aphaenea*, *A. monticola*, and *A. barbata* are all fluvial species and presumably have the same basic spawning habit. *A. lacustris*, on the other hand, lays floating eggs which drift to the shore of Lake Pátzcuaro where they develop in the presumably warmer and more protected water. We consider the spawning habits of this species to be derived and recognize two states of character 18.

0 = spawns in fluvial environment

1 = lays pelagic eggs in lacustrine environment

19. MEDIAN LATERAL SCALES.—Although the frequency distributions of the number of median lateral scales are broadly overlapping, we recognize two states of character 19.

0 = mean value of median lateral scales less than 80

1 = mean value of median lateral scales more than 80

20. UROHYAL BONE: VENTRAL OUTLINE.—This character is somewhat variable but the typical conditions form a clear morphocline. The shape of the urohyal in *A. aphaenea* is distinctive (Fig. 15C); this species is assigned to character state 0. *A. monticola avia* from the Rio Chila has urohyals as in *A. aphaenea*, but individuals from the remainder of the range of this form (the majority of our specimens) have this bone in the shape of a tear-drop. In one specimen of *A. tincella* the urohyal was long and slender as in *A. popoche*, (Fig. 15A, character state 2) but in all other individuals we examined, it tended to be ovate. Thus, *A. monticola*, *A. barbata*, *A. tincella*, and *A. lacustris* are all assigned to character state 1.

0 = short, broad

1 = tear-drop shaped to ovate

2 = long, very narrow

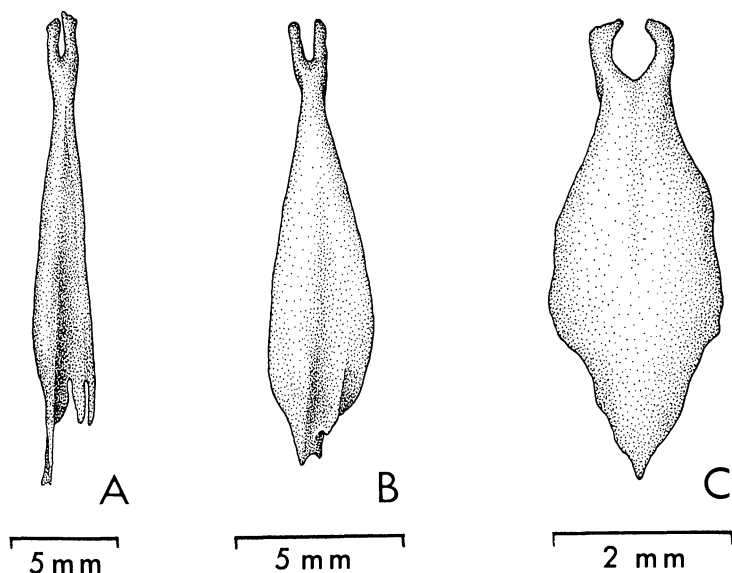


Fig. 15. Ventral view of urohyals of three species of *Algansea*: (A) *A. popoche*, 180 mm, UMMZ 179704-S; (B) *A. tinella*, 145 mm, UMMZ 179752-S; (C) *A. aphanea*, 76.5 mm, UMMZ 192196.

21. UROHYAL BONE: ANTERIOR BIFURCATION.—The shape of the anterior end of the urohyal falls into two character states (Fig. 15). *A. monticola avia* varies as in character 20 and is placed in state 1.

- 0 = arms short, stout, curved mesially
- 1 = arms slender, directed anteriorly

22. SUPRAETHMOID BONE: ORIENTATION.—

- 0 = tilted sharply anteroventrally
- 1 = horizontal
- 2 = tilted anterodorsally

23. NEUROCRANIUM: SHAPE OF DOME IN POSTERIOR VIEW. (Figs. 11, 12).—

- 0 = rounded
- 1 = flattened
- 2 = angular

24. MAXILLA: LENGTH OF ROSTRAL PROCESS. (Fig. 16).—

- 0 = short
- 1 = long

25. MAXILLA: RELATIVE HEIGHTS OF ASCENDING AND PALATINE PROCESSES. (Fig. 16).—

- 0 = unequal, palatine process shorter
- 1 = equal

26. PHARYNGEAL ARCH: RATION OF ANTERIOR LIMB LENGTH TO POSTERIOR LIMB LENGTH.—

- 0 = less than 1.2
- 1 = greater than 1.2

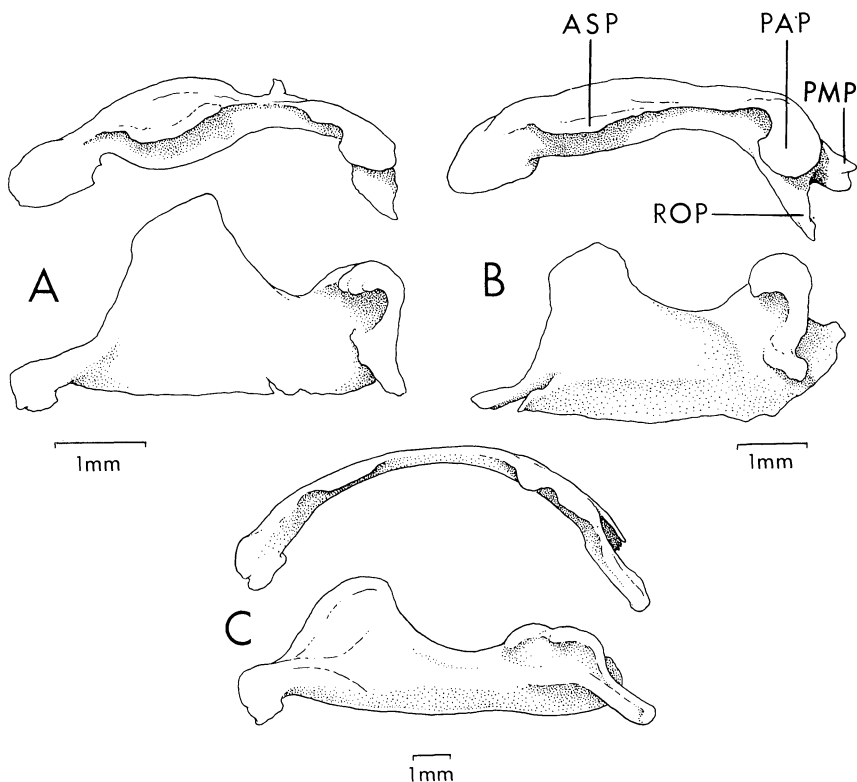


Fig. 16. Dorsal and mesial views of maxillae of three species of *Algansea*: (A) *A. tincella*, 72.7 mm, UMMZ 192475; (B) *A. aphaea*, 76.5 mm, UMMZ 192196; (C) *A. popoche*, 153 mm, UMMZ 179704-S. For abbreviations see text (MATERIALS AND METHODS).

GENERIC STATUS OF *XYSTROSUS*

Xystrosus was erected as a monotypic genus by Jordan and Snyder (1900) for *A. popoche* largely on the basis of its low flat interorbital space, terminal, oblique mouth, lack of barbels, high number of long, slender gill rakers, 4-4 dental formula, long alimentary canal (twice the length of the body), 61 lateral scales, and its lack of pseudobranchiae (this was in error; pseudobranchiae are well developed). *Xystrosus* was said to be allied to *Notropis*, but differing in its "long gill rakers, small scales and the absence of pseudobranchiae." We have found that *Xystrosus* shares numerous features with *Algansea* and also has a number of morphological features which, while striking, could easily have been derived from character states present in species of that genus. Some of Jordan and Snyder's characters are important for distinguishing the type-species, *X. popoche*, but are not diagnostic at the generic level. Thus, for these reasons, given in detail below, we synonymize *Xystrosus* with *Algansea*.

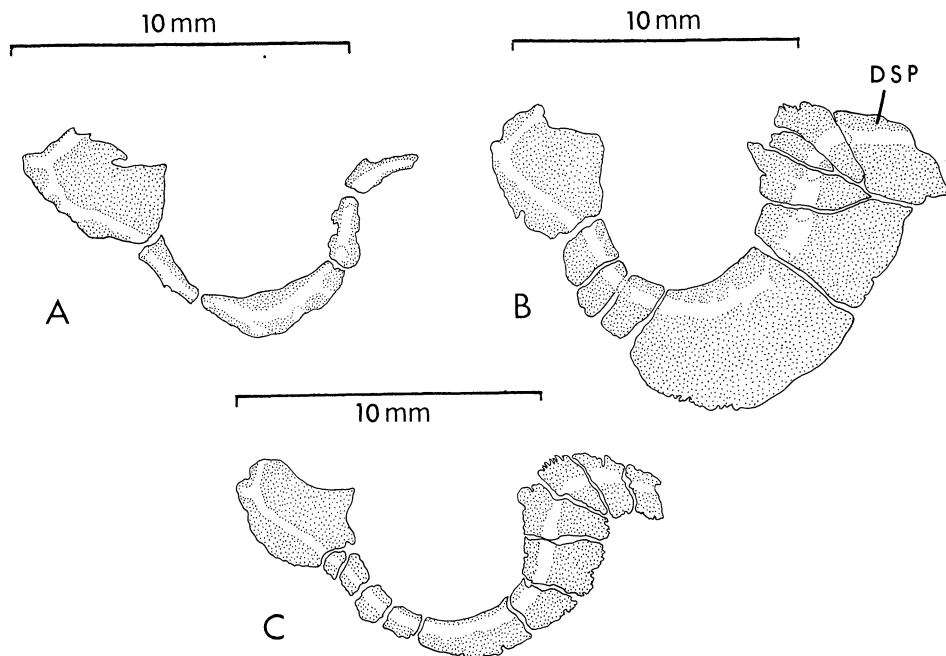


Fig. 17. Infraorbital series of three species of *Algansea*: (A) *A. aphanea*, 81.5 mm, UMMZ 178163; (B) *A. tincella*, 104.5 mm, UMMZ 192246; (C) *A. lacustris*, 88.0 mm, P 2151. For abbreviations see text (MATERIALS AND METHODS).

Jordan and Snyder were undoubtedly impressed by the trophic specializations of *A. popoche* and chose to underscore these adaptations by placing it in its own genus. This tendency to emphasize differences was common among early workers who were faced with the problem of classifying large numbers of new forms at a time when the typological species concept was prevalent. Present emphasis on classifications which reflect historical relationships tend to deemphasize differences between species in favor of recognizing the correct branching sequence of a phylogeny. There are, however, situations where it can be argued that diversity should be recognized (see remarks by C. D. Michener and C. Koopman in Discussion of Symposium Papers on Contemporary Systematic Philosophies, *Syst. Zool.* 22(4):395-96, 1973), and because of this we must determine as objectively as possible the position of *A. popoche* relative to any pattern of character variation that might exist within the genus.

A number of ordination techniques are available (principal component and principal coordinate analysis and nonmetric multidimensional scaling) which can be used to identify species clusters and patterns of variation in reduced character space without, it is hoped, undue distortion and loss of information. Of these, we have chosen to present a principal coordinate analysis of our data, i.e., the calculation of the principal components of an OTU X OTU average distance matrix,

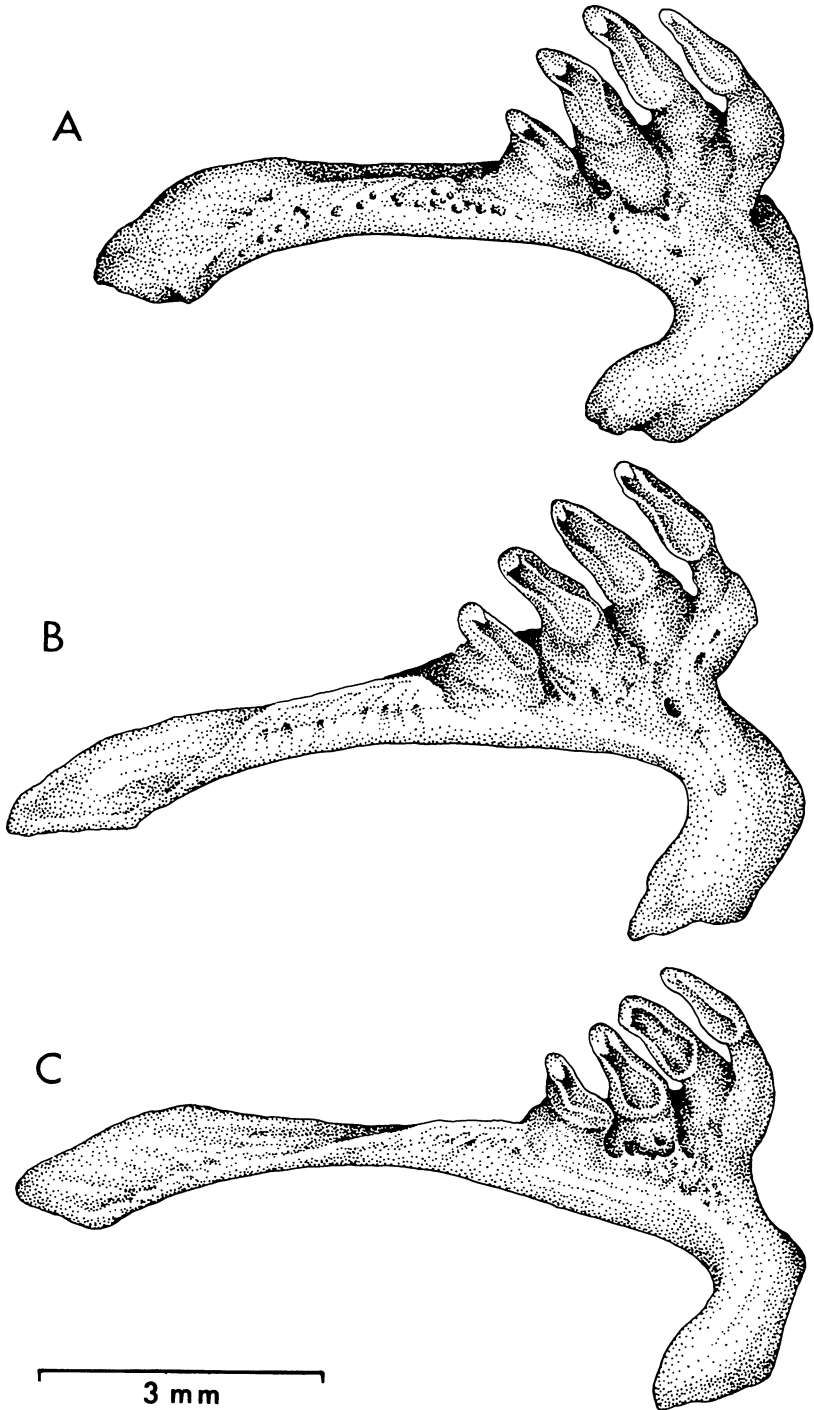


Fig. 18. Dorsal aspect of left pharyngeal arch of two species of *Algansea* and their hybrid: (A) *A. tincella*, 91.0 mm, TU 31961; (B) *A. tincella* x *A. popoche*, 91.5 mm, TU 82781; (C) *A. popoche*, 91.5 mm, UMMZ 167717.

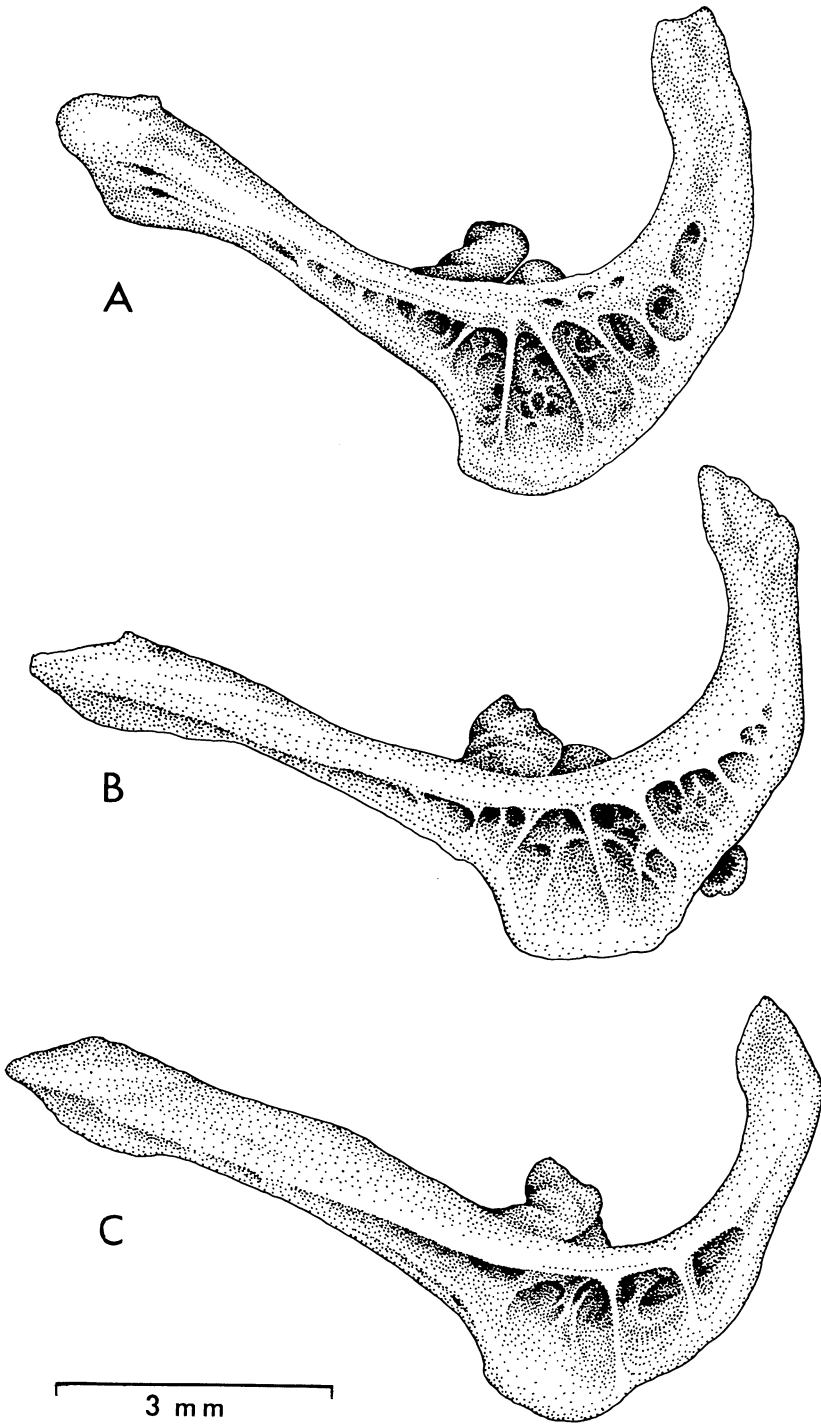


Fig. 19. Lateral aspect of left pharyngeal arch of two species of *Algansea* and their hybrid. Specimens as in legend for Fig. 18.

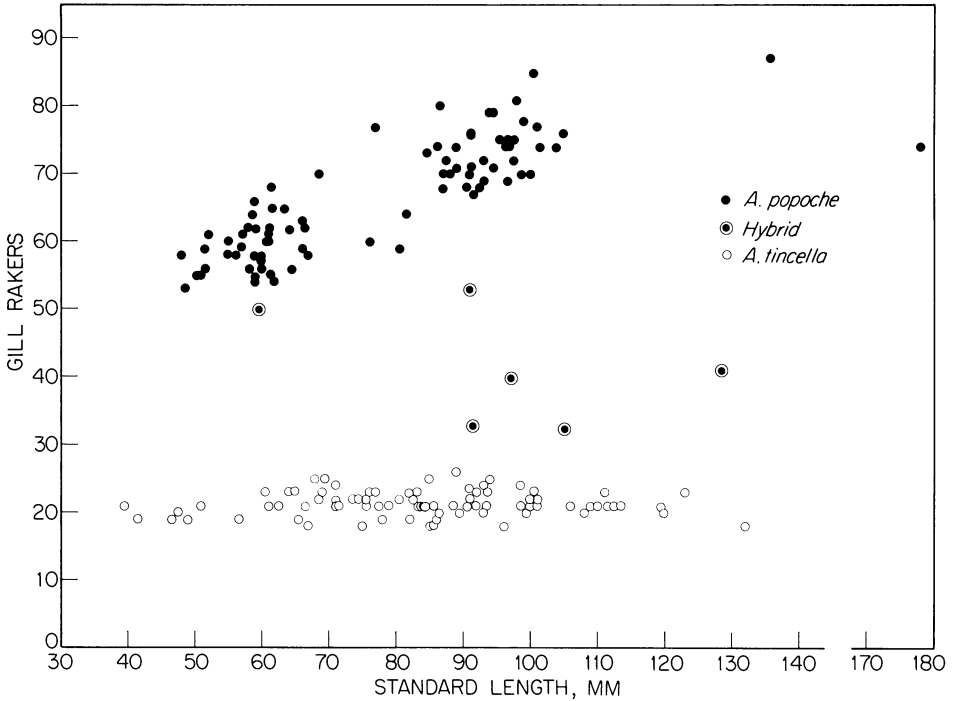


Fig. 20. Gill-raker number in *Algansea popoche*, *A. tincella* (L. Chapala basin only), and their six presumed hybrids (1 from FMNH 16531; 3 from TU 82781, 82782; 2 from UMMZ 193676).

Table 8 (Ciochon and Corruccini, 1977; Sneath and Sokal, 1973; Rohlf, 1972; Green and Carmone, 1970; Sokal and Rohlf, 1970). Rohlf (1972) suggests that this method is preferable to principal components analysis when there are fewer OTU's than characters and/or missing data. The results of a nonmetric multidimensional scaling analysis are not discussed because they do not result in taxonomic insights beyond those presented below. (R. J. Jensen and C. D. Barbour, in prep., have subjected the *Algansea* data to a variety of numerical phenetic and phyletic analyses including the ordination techniques mentioned above, compatibility analysis, the calculation of Wagner trees, and cluster analysis. The results of this study will be discussed elsewhere.) Our calculations were carried out at the Wright State University Computing Center using a recent version of the NT-SYS program (written by F. J. Rohlf, J. Kispagah, and D. Kirk in 1974).

PRINCIPAL COORDINATE I.—All but nine of the characters have moderate to high loadings on the first axis which accounts for 56% of the variation and has an eigenvalue of 9.0 (Fig. 21, Table 7). This phenetic variation reflects major morphological patterns and certain species differences within *Algansea*. Characters 2, 3, 5, 7, 8, 10, 20, 22, and 23 define most of the morphoclines extending between *A. aphanea* (a species

TABLE 8
AVERAGE TAXONOMIC DISTANCES¹ BETWEEN THE SPECIES OF *ALGANSEA*

	<i>aphanea</i>	<i>monticola</i>	<i>barbata</i>	<i>tincella</i>	<i>lacustris</i>
<i>aphanea</i>	0.0				
<i>monticola</i>	1.241	0.0			
<i>barbata</i>	1.383	0.655	0.0		
<i>tincella</i>	1.448	0.645	0.883	0.0	
<i>lacustris</i>	1.690	1.057	1.294	0.838	0.0
<i>popoche</i>	2.357	1.746	1.896	1.434	1.490

¹Sneath and Sokal (1973:124).

unknown to Jordan and Snyder) and *A. popoche* through a central cluster of species. Character states unique to *A. aphanea* (12, 14, 21, and 25) also have high loadings and further separate that species from the other members of the genus. The presence of posterolateral projections from the frontals of *A. barbata* (15) has a moderately high loading on the first coordinate but results in very little separation of that species from *A. monticola*. Finally, the cumulative positive and negative loadings on the first coordinate has resulted in a division of the genus between *A. monticola* and *A. tincella*.

The distribution of the species along coordinates II and III reflects differences and similarities between species rather than morphological trends.

PRINCIPAL COORDINATE II.—The second axis has an eigenvalue of 3.1 and accounts for 19.1% of the variation (Fig. 21, Table 7). *A. lacustris* differs sharply from *A. tincella* (and from all other species of *Algansea*) in its spawning habits (18) and high number of median lateral scales (19). Characters 9, 13, 17, 24, and 26 all combine to produce the strong displacement of *A. popoche* even though each one has only a moderately high loading on this coordinate. Finally, the anterior end of the urohyal (21) and, again, the shape of the frontals (15) are major factors contributing to the displacement of *A. aphanea* and *A. barbata*, respectively.

PRINCIPAL COORDINATE III.—The third axis has an eigenvalue of 3.0 and explains 18.3% of the variation (Fig. 22, Table 7). Moderately high and high loadings for characters 1, 4, 6, 15, 18, 19, and 21 have moved *A. popoche* much closer to *A. tincella* and/or *A. lacustris*. On the other hand, the high loading of character 15 has greatly displaced *A. barbata*. Finally, similarities in the states of characters 15, 18, and 19 have pulled *A. aphanea* close to *A. tincella*, *A. lacustris*, and *A. popoche*.

PRINCIPAL COORDINATES IV AND V.—The fourth and fifth axes have eigenvalues of 0.6 and 0.5 respectively and account for the remaining 6.6% of the variation. We can find no clear, biologically significant patterns among these two remaining vectors.

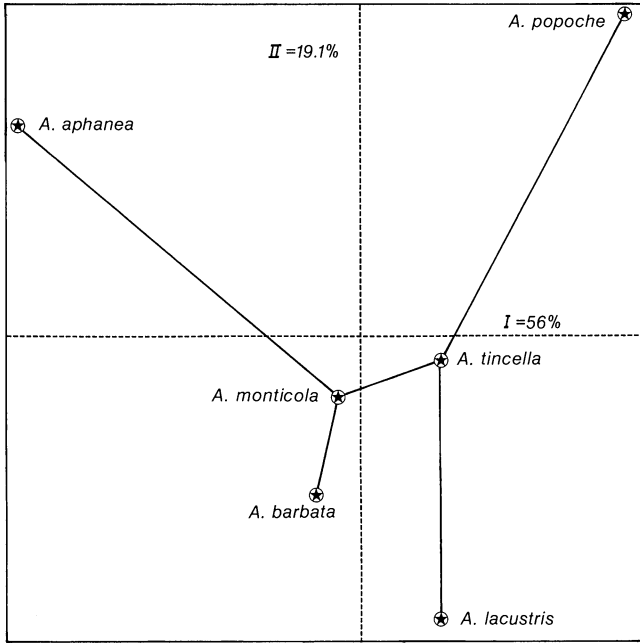


Fig. 21. Projection of OTU's according to factor scores for the first two principal coordinates. Connecting lines represent the shortest average distance between the species in total character space (Table 8).

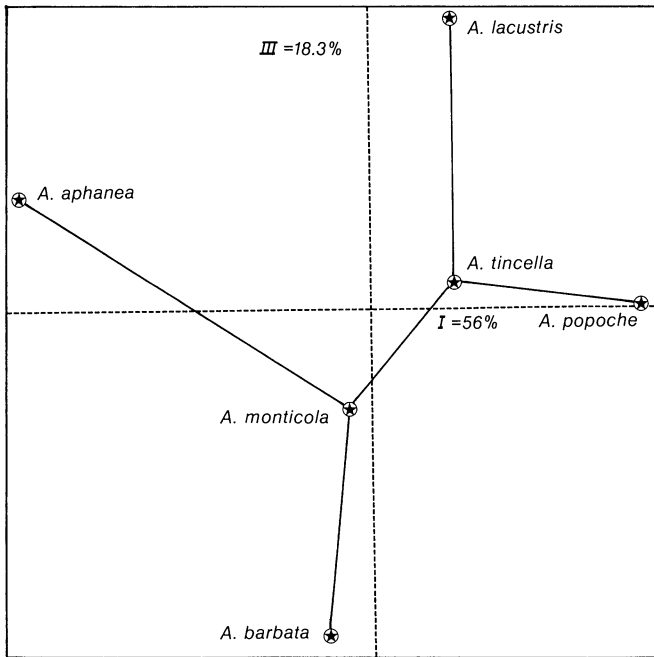


Fig. 22. Projection of OTU's according to factor scores for principal coordinates I and III. Connecting lines as in Fig. 21.

Our analysis indicates that *Algansea* is not a phenetically homogeneous group with *A. popoche*, the expected morphologically distant outlier, but rather a diverse assemblage whose species are held together by morphoclines. If our goal were the recognition of diversity (and by so doing the creation of morphologically uniform taxa), logic would compel us not only to retain *Xystrosus*, but also to recognize *A. aphaenea* and perhaps *A. lacustris* at the generic level as well. Such a course is unsatisfactory. In the words of Bolin (1947): “. . . splitting of this type does not represent an increase in knowledge, but simply a destruction of all indication of relationship.” It appears, then, that the best course of action from the simple phenetic standpoint would be to regard all of the species as congeneric. This decision is, of course, completely arbitrary, but we see no other reasonable way of interpreting the results of our analysis.

Phylogenetic considerations reveal that the plate-like dermosphenotic (Fig. 17) present in *Algansea* is, except for *Gila crassicauda* (Baird and Girard), and three members of the subgenus *Temeculina* of *Gila*, apparently unique among western North American cyprinids. We consider this strong evidence that *Algansea* is a monophyletic group. (The relationship of *Algansea* to *Gila* is discussed below.) Also, it is apparent that *A. popoche* shared a common ancestor with *A. tincella* and *A. lacustris*. As we have seen above, most of the former species' specializations are simply more extreme expressions of character states already present in *A. tincella* and *A. lacustris*. That they could have arisen independently strikes us as highly unlikely.

On the basis of both phenetic and cladistic evidence, we can find no compelling argument for the retention of *Xystrosus* as a separate genus. The major evolutionary division within the genus lies not between any of the more specialized forms and the remaining species, but rather between *A. aphaenea*, *A. monticola*, and *A. barbata*, on the one hand and *A. tincella*, *A. lacustris*, and *A. popoche* on the other (see below, PHYLOGENY OF *ALGANSEA*).

PHYLOGENY OF *ALGANSEA*

Among the Nearctic cyprinids which we examined the only ones that share a plate-like dermosphenotic with *Algansea* are *Gila crassicauda* (Baird and Girard), as figured in Miller (1963), and three other species in this genus corresponding in part to the subgenus *Temeculina* Cockerell (Miller, 1945): *G. orcutti* (Eigenmann and Eigenmann), *G. purpurea* (Girard), and *G. ditaenia* Miller. *Gila pulchra* Girard, the fourth member of this subgenus, has a dermosphenotic which is not as wide as the others. As far as we can tell, a plate-like dermosphenotic is not found in any other native western North American cyprinid, an observation which, if true, suggests that *G. crassicauda* should be included in the

subgenus *Temeculina* and that there is a relationship between these species and *Algansea*.

The distribution of these five species of *Gila* complements that of *Algansea*. *Gila crassicauda* is restricted to the Sacramento-San Joaquin river system of central California, and is now believed to be extinct. The distribution of the *Temeculina* species group (Fig. 1) extends from southern California to northwestern México. All species occur in small streams or in tributaries to larger rivers. *Gila orcutti*, the northernmost form, naturally occurred only in coastal streams of southern California. *Gila ditaenia* is found only in the Río Magdalena drainage of extreme northwestern Sonora and extreme southern Arizona. *Gila purpurea* has a localized distribution in certain tributaries to the Río Yaqui, in southeastern Arizona and Sonora, at lower levels on the western slope of the Sierra Madre Occidental below 1,333 m, where it may be syntopic with *G. robusta* Baird and Girard. It also inhabits the independent drainages of the Río Sonora above Hermosillo and the Río Matape above Guaymas. *Gila pulchra* is the only species of the group that occurs on both slopes of the Sierra Madre Occidental. It has been taken in the headwaters of the Yaqui near Miñaca, the upper part of the Río Mayo, and in the Río Verde, a headwater of the Río Fuerte, all in Chihuahua. The species also occurs in the upper Río Conchos, a tributary to the Río Grande. As the western Sierra Madre had its origin at the beginning of the Tertiary, suitable habitat has probably been continuously available in northwestern México for these species and their ancestors. Their distributional limits and dispersal rates are probably functions of climate and stream piracy.

On the basis of these observations, we are confident that the evolutionary affinities of *Algansea* lie with *Gila* rather than with any other group of North American cyprinids. The evidence presented above suggests that *Algansea* and the subgenus *Temeculina* of *Gila* (including *G. crassicauda*) may be sister groups. If this should be correct then future studies may result in a realignment of the taxa presently included in these genera.

We surmise that the ancestor of *Algansea* was widespread in montane western México during the latter part of the Tertiary, perhaps occurring from the southern terminus of the present distribution of *Gila pulchra* to as far south as the ranges of *A. monticola avia* and *A. aphanea*. Two lineages diverged from this stock, one leading to the small, predominantly lotic species and the other giving rise to three forms that have invaded lacustrine environments and reach larger sizes.

The ancestor of the small barbelled forms ranged from at least as far east as the present distribution of *A. barbata* in the headwaters of the Río Lerma (Valley of Toluca) westward through the present ranges of *A. monticola* and *A. aphanea*. Its preferred habitat was likely that of moderately swift to swift upland streams and rivers which drained into the ancestral premid-Pleistocene uplift river basin (see Barbour, 1973b,

and Smith, Cavender and Miller, 1975, for comments on the geological history of the Lerma drainage). *Algarsea monticola* has the most primitive character states and thus appears to be the closest to the ancestral form. *A. monticola monticola* is known only from the ríos Colotlán and Juchipila, northern tributaries to the Río Grande de Santiago. *A. monticola avia* occurs in the state of Nayarit from streams in the vicinity of Santa María del Oro west to Tepic and south to the Río Chila basin. Recession of the ancestors' range to that presently occupied by *A. monticola* is probably associated with habitat changes, including the formation of lacustrine systems, changing fish community structure and desiccation, which occurred during and after the uplift. The division of the ancestor into two subspecies separated by the Río Grande de Santiago is most likely correlated with the increase in the torrential nature of the river as it eroded into the slowly elevating plateau.

Each of the subspecies of *A. monticola* shares at least one derived character state with one of the other two barbelled forms. This coincidence strongly suggests that these species, *A. aphanea* and *A. barbata*, are derived from peripheral, isolated populations of the formerly widely distributed ancestor.

It is characteristic of *A. aphanea* that the frontals do not suture with the pterotics. A tendency toward this condition was also present in one individual of *A. monticola avia* from the Río Chila basin (compare Figs. 9A and B). This appears to be the same specialization even though in the former species the gaps are filled by finger-like extensions of the parietals and in the latter by exposed portions of the sphenotics. We interpret this similarity as an indication that *A. aphanea* and the southern populations of *A. monticola avia* shared a common ancestor at some time in the past. If the state of the urohyal (Fig. 15C) which the Río Chila populations also share with *A. aphanea* turns out to be derived, it will further strengthen our conclusion.

A. aphanea is the most divergent of the three lotic species. Its sub-terminal mouth and dorsolateral placement of the eyes suggest benthic adaptation. The loss or reduction of the epiotic arches suggests changes in the attachment of the epaxial muscles to the back of the skull, which may be related to a shift from a mid-water to bottom-dwelling habitat. Other adaptations are directed toward modification of the jaws and suspensorium. These include changes in the relative lengths of the maxillary processes (Fig. 16B), an extreme lateral flexure of the biting surface of the gnathic rami (Fig. 14C), a short, wide urohyal mentioned above, and, if they fall beyond the range of variation found in *A. monticola*, an enlarged and more posteriorly directed articular facet of the articular bone (Fig. 14C) and a shortening and widening of both the symplectic and the arm of the quadrate. Finally, *A. aphanea* is the only member of the genus with reduced infraorbital bones (Fig. 17A).

Algarsea aphanea inhabits the Río Ayutla, a headwater of the Río Armería, and small tributaries of the Río Coahuayana basin (Fig. 2).

The Río Ameca, which supports a variety of goodeids and *A. tincella*, represents a distributional hiatus for these smaller barbelled forms.

The secondary flexure of the intestine which is characteristic of *A. barbata* (Fig. 3B) is also found in a few individuals of *A. monticola monticola*, suggesting that these two forms also share common ancestry. *A. barbata* is apparently a relict of the eastern populations of the ancestral form and is restricted to the headwaters of the Río Lerma and contiguous areas in and near the Valley of Toluca. Its presence in this compartment of the Río Lerma with two other endemic species, an atherinid, *Chirostoma riojai* Solórzano and López, and a goodeid, *Girardinichthys multiradiatus* (Meek), suggests that this area has been an isolated basin during part of its history. The lacustrine history of the region may explain *A. barbata*'s larger size, smaller scales, and possibly the greater number of preoperculummandibular pores.

The phylogeny of *Algansea aphanea*, *A. monticola*, and *A. barbata*, derived according to the method of Hennig (1966), is presented as the left branch of Fig. 23. Given our lack of knowledge concerning the details of the geological events associated with the formation of these three species, we consider this to be an acceptable estimate of their evolutionary relationships. Two further points should be made, however. First, if we are correct in assuming that the populations which were to give rise to *A. aphanea* and *A. barbata* were isolated during the mid-Pleistocene uplift, then there is a chance that these events took place at essentially the same time. Given the fact that species exist in space as well as time, there is no reason why an ancestral form ranging throughout a tectonically active (or any other) region cannot give rise to several descendents simultaneously. The degree of differentiation of each resulting species would be a function of the severity of selection pressures, biological as well as physical. That systematists do not usually have the resolving power to view the isolation of ancestral populations does not mean that it always has to be a dichotomous event. Unresolved trichotomies may indeed be unresolved; they may also be nothing more than an *a priori* assumption of an overly rigid taxonomic methodology.

The second point that we wish to emphasize is that sister group relationships among the barbelled forms are between taxa of unequal rank, species and subspecies, a fact that is obscured when relationships are portrayed at the species level as in Fig. 23. If this goes against the grain of rigid Hennigian cladistics, it should serve as a reminder that nature does not always snugly fit the models constructed by the biologist. In this particular case, the ancestral form has differentiated into two subspecies which still preserve evidences of earlier speciation events.

The second lineage within *Algansea*, species which lack barbels and reach a greater body length, may have originated in base-level streams and rivers, springs, or lakes along the southeastern foot of the Sierra

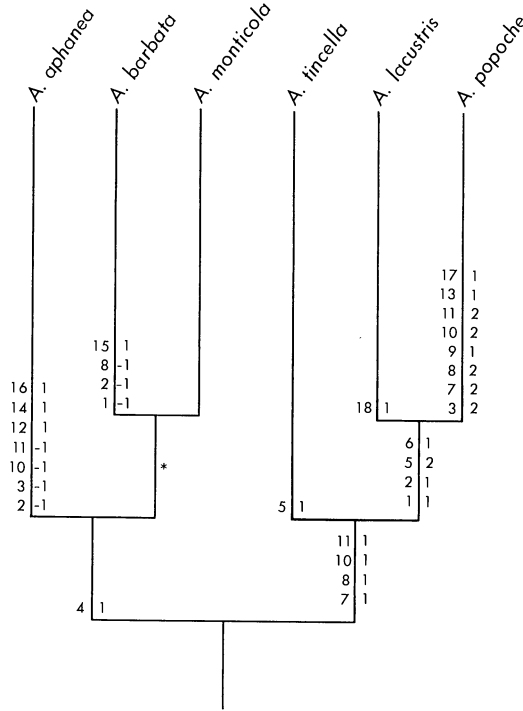


Fig. 23. Phylogeny of the species of *Algansea* inferred from the distribution of shared specializations. Characters are identified by numbers to the left of the lines, derived character states by numbers to the right. *The lack of a derived character state indicating a phylogenetic relationship between *A. barbata* and *A. monticola* is an artifact of character coding. The unique gut-coiling pattern of *A. barbata* is also present in a minority of the individuals of *A. monticola monticola* that we examined.

Madre Occidental. With the development of a convoluted intestine, suggesting the ability to shift to a more herbivorous diet, and an increase in the number of gill rakers, head sensory pores, and other meristic characters, this presumably Tertiary form was likely tolerant of a variety of aquatic habitats and perhaps became widespread in the ancestral Río Lerma drainage and contiguous basins to the north. *Algansea tincella* is the modern representative of this precursor and occupies essentially the same phylogenetic position in *Algansea* as does *C. humboldtianum* in *Chirostoma*. In dorsal outline of the neurocranium, relative robustness of the maxilla, mandible, quadrate, and symplectic, lateral flexure of the gnathic ramus, lateral position of the eyes, and, generally, in the relative size and proportions of the pharyngeal arch and teeth, *A. tincella* is essentially the same as *A. monticola* and *A. barbata* (with the exception of the latter's lateral expansions of the frontals). Ovate urohyals are found in both *A. tincella* and *A. barbata*, a shape very similar to the tear-drop form found in *A. monticola*.

Algansea tincella is widespread in the Lerma basin where it shows some interesting patterns of variation (see SPECIES ACCOUNTS).

Its presence in the Valley of México, the Lake Cuitzeo basin, and the Valley of Tocombo south of Lake Chapala is further evidence that these interior drainages were once part of the Río Lerma system. If *A. tincella* occurred in basins to the north of the present Lerma drainage, its demise in this part of its range is probably related to the increasing post-Pleistocene aridity that eliminated aquatic habitats and to shifting drainage patterns that brought an influx of competing northern species (e.g., *Gila conspersa* Garman) from the Río Grande basin.

The remaining species, *Algansea popoche* and *A. lacustris*, are lacustrine forms inhabiting lakes Chapala and Pátzcuaro, respectively. The ancestor of the latter was probably isolated in the Lake Pátzcuaro basin during the uplift. This species, along with four species of *Chiostoma* and three goodeids, is convincing evidence that the present Lake Pátzcuaro, now an interior drainage, was once connected to the Lerma system. *A. lacustris* is not present in Lake Zirahuén, about 40 km to the south, even though the fish fauna of that lake is derived from species present in Lake Pátzcuaro.

Algansea lacustris has a very high number of median lateral scales and lacks or has obsolescent radii on the anterior field of its scales. Other than these differences and the upturned position of its lower jaw, it is essentially the same as *A. tincella* in every other morphological feature that we studied. Unlike *A. tincella*, however, it reaches its spawning peak during the winter and early spring (De Buen, 1941, 1944). The female lays floating eggs which drift to the shore where they develop in the warmer, shallower water. *Algansea tincella* spawns in streams during the summer months.

A. popoche is the most morphologically specialized of this species group. The extreme development of the epiotic arches, the appearance of ridges at the base of the supraoccipital crest, and the broad, lateral wings of the exoccipitals with their lateroventral margins slightly developed into posteriorly directed flanges, all suggest alterations in epaxial muscle attachments, perhaps associated with a shift in habitat from stream to lake. Radii are also lacking on the anterior scale fields; they are never obsolete, as they may be in *A. lacustris*. Other modifications are more directly trophic: the obliquity of the lower jaw and the attenuate arm of the pharyngeal arch (both more extreme than in *A. lacustris*), the slender dentary and maxilla, the weak pharyngeal process of the basioccipital and its reduced masticatory surface, weak pharyngeal teeth, long and numerous gill rakers, and the highly coiled gut.

Although *A. popoche* is now restricted to Lake Chapala and adjacent parts of the Río Lerma and Río Grande de Santiago, it probably also occurred in nearby basins (lakes Atotonilco, Magdalena, Cajititlán, Zacoalco, and Sayula) during post-uplift time. Our evidence of a wider distribution is the observation by Tamayo and West (1964) that now nearly dry Lake Magdalena, near Ezatlán, Jalisco (see Barbour, 1973b, Fig. 2, loc. 4) supported a fishery for the larger species of *Chiostoma*

(pescado blanco) around 1900. We feel that if the larger atherinids were present, it is probable that *A. popoche* was as well. Factors which probably preclude its presence in these areas, short of complete desiccation, may be their shallowness, excessive turbidity, and probably higher salinity. The scarcity of streams suitable for spawning may also be a factor.

The evolutionary relationships of *A. tincella*, *A. lacustris*, and *A. popoche* may be interpreted in two different ways. The first and most parsimonious phylogeny is presented as the right branch of Fig. 23. According to this version, the late Tertiary ancestor gave rise to two species, one leading to the present-day *A. tincella* and the other, a common ancestor of *A. lacustris* and *A. popoche*. This latter form reached a larger size, had an upturned mouth, an increased number of preoperculomandibular pores and scales with radii which were obsolete or absent on the anterior field. It was probably widely distributed prior to the uplift, during which time it became extinct throughout its range except for populations isolated in the Lake Pátzcuaro and Chapala basins.

In spite of the above reasoning and the reliance on parsimony as a guiding principle in phylogenetic analysis, it can be argued that characters 1, 2, 5, and 6 are weak indicators of a sister species relationship between *A. popoche* and *A. lacustris* and actually represent independently evolved adaptations to a lacustrine environment. Increases in body size (1) and the number of head pores (5) are commonly associated with the invasion of lakes by fishes and could have easily evolved twice. In a like manner, the loss of radii on the anterior scale fields (6) appears to be a trivial lacustrine adaptation that could occur independently in *A. popoche* and *A. lacustris*. We also note that the separation of *A. tincella* from the lineage leading to the other two species on the basis of differences in the states of characters 1 and 2 is, in part, an artifact of coding. *A. tincella* was assigned to the primitive state for character 1 (standard length) because the majority of our specimens are less than 100 mm S.L. However, when this species occurs in lakes (e.g., Lake Xochimilco, Valley of México, and Lake Zacoalco, Jalisco) it may reach 174 mm S.L. The largest individuals also show an upturned lower jaw (2) which approaches that of *A. lacustris*. We, therefore, suggest (and favor) as a reasonable alternative that *A. lacustris* and *A. popoche* evolved independently from isolated populations of an *A. tincella*-like ancestor, and that the character states they hold in common evolved in parallel (Fig. 24). These events would have occurred during the isolation of the Chapala and Pátzcuaro basins, perhaps during the uplift, and have the added advantage of not requiring the evolution of a widespread lake-adapted common ancestor. This phylogeny, however, exposes two additional problems. First, *A. tincella* and *A. lacustris* share no uniquely derived character states. Although further study may uncover such states, we note with interest that the difficulty

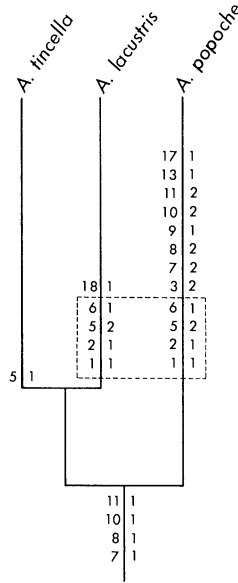


Fig. 24. Alternative phylogeny of *Algansea tincella*, *A. lacustris*, and *A. popoche*. Characters and character states as in Fig. 23; those enclosed by rectangle evolved in parallel. See text for discussion.

is resolved if it is assumed that *A. popoche* and *A. lacustris* were isolated more or less simultaneously. The second problem involves the many specializations of *A. popoche*. If *A. lacustris* and *A. popoche* evolved in approximately the same time-span, is there any evidence of increased selection pressure which would accelerate the divergence of this species?

Barbour (1973b) suggested that ecological interactions have had a pronounced effect on the distribution of *Chirostoma*. While reviewing our data for morphological patterns which might be open to a similar interpretation, we were struck by the fact that most of the carnivorous¹ forms, *A. monticola* and *A. aphaea*, occupy ranges at the edge of the Mesa Central (Fig. 2) in spite of what appears to be suitable habitat within the Lerma basin (e.g., Río Duero, Michoacán, tributaries to the mid-section of Río Lerma in the Bajío region, headwaters of the Río Turbio, Jalisco and Guanajuato, and the Río Verde, northeast of Guadalajara, Jalisco). The only member of this species group which occurs in the Lerma drainage proper, *A. barbata*, has a slight secondary flexure in the gut (present only occasionally in *A. m. monticola*), and the most widespread species, *A. tincella*, has a variable but pronounced flexure. We suggest that competition for food between *Algansea* on one hand and *Chirostoma* and the goodeids on the other may have prevented the occurrence of a moderate-sized carnivorous minnow in the

¹We assume here that species with short guts will tend to be more carnivorous and those with long guts will tend to be more herbivorous.

central part of the Lerma basin. Considering only the major components of the fish communities (Goodeidae and Atherinidae), *A. aphanea* lives only with the goodeids *Allodontichthys* and *Ilyodon*, and *A. monticola avia* coexists only with two goodeids, *Goodea atripinnis* and *Xenotoca eiseni*; *A. m. monticola* is sympatric only with *G. atripinnis*. *Algansea barbata*, on the other hand, has been taken with *Chirostoma riojai* and *Girardinichthys multiradiatus*, and *A. tincella* occurs with a variety of atherinids and goodeids throughout its range. By the same reasoning, the selection pressures which resulted in the evolution of an herbivorous filter-feeder (*A. popoche*) in the ancestral Lake Chapala basin may have stemmed, at least in part, from the presence of a diverse assemblage of atherinids which, as speciation progressed, utilized the entire spectrum of available prey. Under these conditions it is easy to picture the progressive and rapid ecological and morphological specialization of the ancestral *A. popoche* as the number of species of *Chirostoma* in the lacustrine community gradually increased (8 or 9 species currently coexist in Lake Chapala). *Algansea lacustris*, in spite of its reproductive adaptations to a lake environment, appears to be more generalized in its food habits, at least as reflected in its morphology. From an evolutionary standpoint it may be significant that the species of *Chirostoma* with the most gill rakers (*C. grandocule*, 28-34, Barbour, 1973a), also occurs in Lake Pátzcuaro and may have blocked the development of another cyprinid filter feeder.

We emphasize that we have no ecological data to support these morphological coincidences. The few stomachs of *Algansea* that were examined contained completely digested, and therefore unidentifiable, food items. We suggest that ecological studies on the trophic relationships of *Algansea*, *Chirostoma*, and the 35 or so species of goodeids are needed to test this hypothesis.

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