Gambusia georgei sp. nov. from San Marcos, Texas

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Three species of *Gambusia* occur sympatrically in the upper San Marcos River; each species occupies a specific habitat. One has not previously been noted in the literature and is herein described as *Gambusia georgei.* The limited hybridization with *G. affinis* does not seem to have reduced the specific integrity of either type. The new species is extremely rare and could be exterminated by minor habitat modifications.

***Gambusia georgei* is a localized endemic inhabiting thermally consistent shallow water over muddy bottom with sparse aquatic vegetation in the San Marcos River. It is differentiated from all other species of *Gambusia* by having more than 5 segments of 4a incorporated into the elbow and by having a compound claw on the end of 4p.**

INTRODUCTION

THE upper San Marcos River has been considered as an area of extensive endemism by Hubbs and Peden (1968), who predicted that additional undescribed endemics might be present. Discovery of another endemic supports our evaluation of the speciose nature of this unique stream segment.

During our analysis of the ecological segregation between *Gambusia affinis* (Baird and Girard) and *G. geiseri* Hubbs and Hubbs we noted that some of our samples of the former were dimorphic. Careful study showed that the two morphs represented distinct species, one of which is endemic and described below.

METHODS

Terminology of Rosen and Bailey (1963) is used. Dorsal counts and head measurements are based on all specimens used in the character index. Other counts and measurements are based on the male holotype, 9 of the 13 male paratypes, and 10 of the 31 female paratypes. Number of specimens possessing each count is enclosed within parentheses after the count. Measurements are expressed as thousandths of the standard length. Range of measurements for each character is presented. Measurement of the holotype is given within parentheses.

Gambusia georgei n. sp.
Figs. 1 and 2

Holotype.—University of Michigan Museum of Zoology 187447 male 29.3 mm standard length captured by Clark Hubbs and Michael M. Stevenson on 7 March 1968, in the San Marcos River at the Highway I-35 bridge, Hays County, Texas. Paratypes, UMMZ 187448, 13 mature males and 31 females collected with the holotype. Ninety-seven other specimens, TNHC 7195, 7196, 7197, 7199, 7201, 7202, 7203, 7204, 7205, 7206, 7207, and 7212, collected from the San Marcos River between Rio Vista Dam and the eastern boundary of the San Marcos State Fish Hatchery 500 m on each side of the I-35 bridge, were also examined.

Two additional females UMMZ 65250 collected by D. S. Jordan and C. H. Gilbert from San Marcos Spring appear to represent *G. georgei.* One mature male (UMMZ 72566) a putative hybrid with *G. affinis* was collected from "San Marcos Spring" by S. W. Geiser on 13 May 1925. Five other hybrids were collected together with the types (UMMZ 187445) and four other male hybrids, TNHC 7208, 7210, 7216, and 7217. The fish were compared with specimens of *G. affinis,* TNHC 7198, 7200, 7209, 7211, and 7213, present in the same collections.

Counts; Male.—Dorsal fin rays, 7 (43), 8 (1); sum of left and right pectoral fin rays, 24 (1), 26 (5), 27 (3), 28 (1); scales in lateral series, 29 (1), 30 (6), 31 (3); scale rows around caudal peduncle, 16 (10).

Counts; Female.—Dorsal fin rays, 6 (1), 7 (66), 8 (1); anal fin rays, 9 (9), 10 (1); sum of left and right pectoral fin rays 26 (9), 27 (1); scales in lateral series 30 (8), 31 (2); scale rows around caudal peduncle 16 (10).

Measurements; Male.—The holotype is 29.3 mm in standard length; 13 paratypes range from 21.3 to 26.3 mm SL. Body depth at origin of dorsal fin, 195–218 (218); dorsal

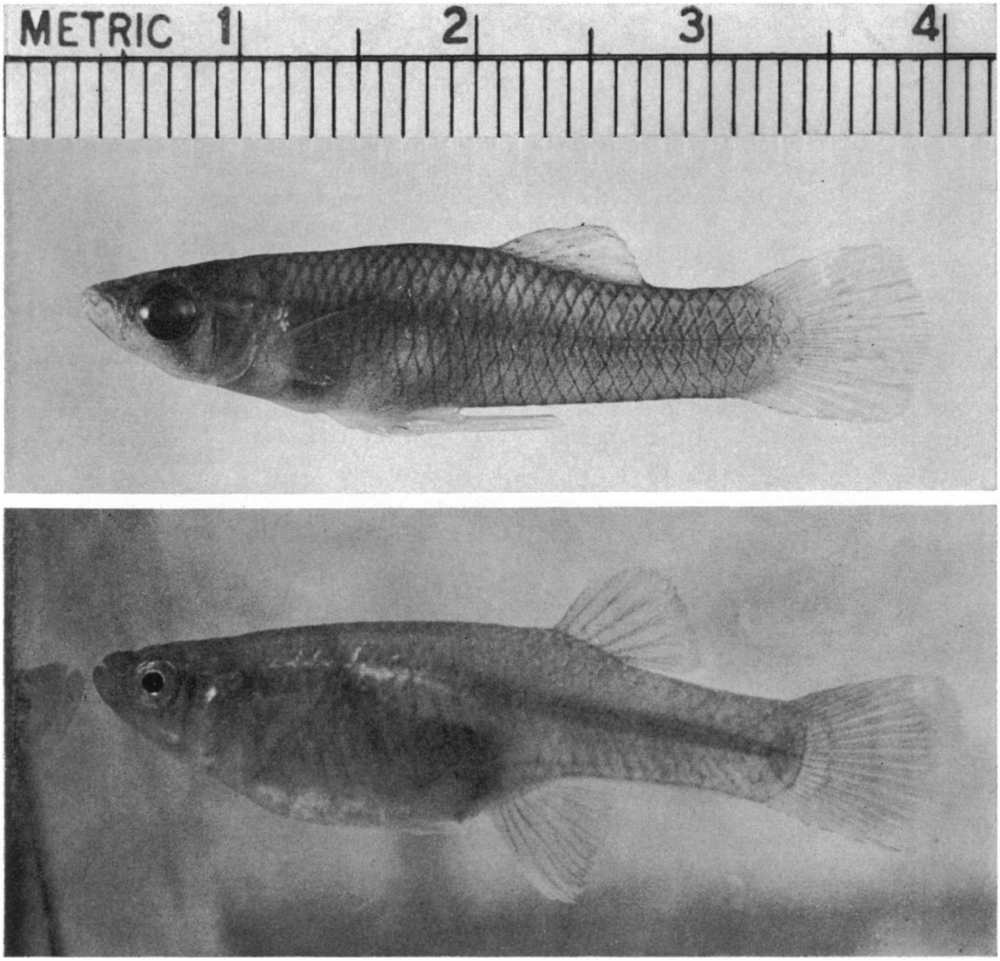

Fig. 1. *Gambusia georgei*, n. sp. upper, holotype; lower, adult female in an aquarium.

fin origin to tip of lower jaw, 577–606 (587); anal fin origin to tip of lower jaw, 429–476 (447); dorsal fin origin to caudal base, 403–431 (427); anal fin origin to caudal base, 539–577 (577); caudal peduncle depth, 139–158 (157); head length, 245–281 (256); head width, 134–164 (147); snout length 95–104 (99); orbit length, 75–86 (75); interorbital bony width, 90–112 (99); mouth width 81–98 (96); depressed dorsal fin length, 220–260 (242); gonopodial length, 279–315 (290); caudal fin length 232–260 (246); pectoral fin length, 184–207 (201); and pelvic fin length, 83–104 (99).

Measurements; Female.—Standard lengths of 31 paratypes range from 25.6 to 39.2 mm. Body depth at origin of dorsal fin 186–212; dorsal fin origin to tip of lower jaw, 620–642; anal fin origin to tip of lower jaw, 545–574; dorsal fin origin to caudal base, 354–406; anal fin origin to caudal base, 431–478; caudal peduncle depth, 134–150; head length, 237–296; head width, 165–179; snout length, 94–114; orbit length, 74–95; interorbital bony width, 114–133; mouth width, 82–119; depressed dorsal fin length, 205–226; depressed anal fin length, 186–206; caudal fin length, 213–253; pectoral fin length, 184–204; pelvic fin length, 95–123.

Gonopodial characters.—The gonopodium is broadly acute. The third ray is moderately bowed over elbow. Eight to ten antrorse slender moderately long spines. Distal spine usually extends to tip of gonopodium. Distal four or five spines with well developed bases. Ray 4a extends almost to distal tip of gono-

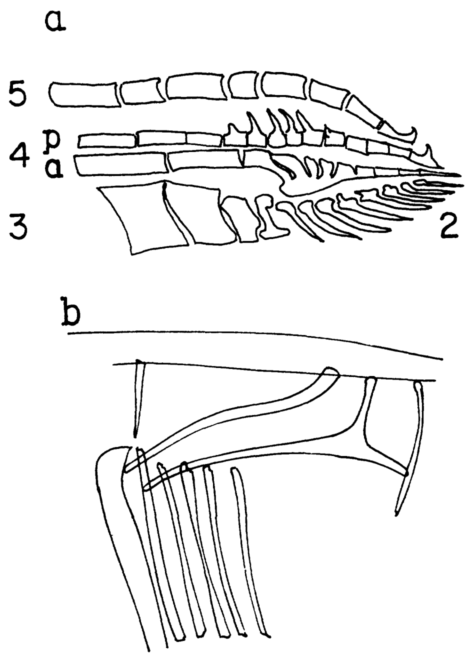

Fig. 2. Diagram of (a) gonopodial tip and (b) suspensorium of *Gambusia georgei*.

podium or occasionally exceeds ray 3. Well developed elbow opposite level of proximal 3rd ray spines. This elbow composed of from five to six enlarged segments which are fused together on their anterior surfaces. Elbow greatly thickened so that there is little space between it and the enlarged bases of the spines on ray 3. Distal two or three segments of ray 4a slender and not fused to each other. Proximal segments of elbow opposite distal one or two serrae of ray 4p. Posterior and anterior branches of ray 4 diverge moderately at level near proximal serra and converge distally. Ray 4p a little shorter than ray 4a. Ray 4p with four or five retrorse long slightly curved serrae. Small retrorse claw or hook on posterior branch of ray 4 with short pointed apex. Anterior branch of ray 5 moderately bowed over serrae and terminating in small J-shaped claw.

Usually two gonopophyses. Occasionally a weakly developed, short third gonopophysis present (perhaps resulting from introgression with *G. affinis*?). First gonopophysis without uncini, its shaft forming an angle of about 40° with vertebral column. Second gonopophysis with well developed uncini. Third caudal vertebra with normal haemal spine (except when it is modified into a short weakly developed gonopophysis).

Color of preserved specimens.—Strongly cross-hatched by dark pigmentation on margin of scale pockets. Area anterior to anal fin and below eye and pectoral fin pale and not cross-hatched. Area from occiput to snout darker. Weak short dusky bar leading postero-ventrally across cheek from lower border of eye. Lower jaw dusky. Operculum dusky. Darker smudge above base of pectoral fin. Mid-dorsal stripe from occiput to base of dorsal fin. Frequently a very diffuse dusky lateral stripe running posteriorly from above base of pectoral fin. This stripe often dissipates before reaching caudal. A few scattered dark crescent shaped markings on lateral side. A very thin mid-ventral dark line running from anal fin to caudal fin.

Darker pigment usually present near base of dorsal fin. This pigment frequently concentrated into a row of subbasal spots. Pigment often concentrated at fork of each branched dorsal ray to form another row of a few faint spots. Distal margin of dorsal fin with dark pigment. Dorsal and ventral margin of caudal fin with thin line of dark pigment. Caudal fin usually plain. A weak concentration of pigment at proximal fork of each branched caudal ray may form a row of a few faint small spots. Rarely, a large female may have a secondary row of very faint spots at level of secondary fork of each branched ray. Anal fin tends to be dusky with a concentration of pigment on the anterior and distal margins. A concentration of dusky pigment may occur on membrane between basal half of posterior five or six anal fin rays. Gonopodia dusky. Darker pigment in the form of thin crescents on each side of the anal and urogenital opening may be present on a few females.

In life, *G. georgei* is usually plainly marked. A behaviorally aggressive fish may have a pronounced development of black on the distal margin of the dorsal fin, on the dusky patch above the pectoral fin, and the black bar on the cheek. This bar can extend itself through dorsal and ventral portions of the usually pale iris. The dark pupil is incorporated into this dark bar. The median fins have a pronounced lemon yellow coloration that provides a ready field identification. In a behaviorally recessive or submissive fish, the above color pattern will disappear and the diffuse dark lateral stripe will develop or become intensified.

We name this species after Dr. George S. Myers because of his extensive contributions to the study of cyprinodont fishes and because of his long interest in problems of endangered fishes such as *G. georgei.*

Relationship to Other Gambusiins

Rosen and Bailey (1963) distinguished the species of *Gambusia* from those of related genera by the thickened upper pectoral rays of mature males. All males of *G. georgei* have this attribute. The gonopodium (and its suspensorium) also agrees with the description by Rosen and Bailey (1963), Rivas (1963), and Hubbs (1926) despite minor differences among these authors as to which species are included in the genus.

It is difficult to use Rivas' key in assigning *G. georgei* to species groups of *Gambusia.* For example, his primary division contrasts two gonopodial structures—long *vs.* short spines on ray 3 and strongly *vs.* weakly coalesced segments in elbow. The gonopodium of *G. georgei* has one attribute of each subsection. If one makes compromises, it is possible to consider that *G. georgei* might belong to Rivas' subgenus *Orthophallus* (only one species, *lemaitrei* which is differentiated from *G. georgei* by the short heavy spines on ray 3 and three gonopodial suspensoria in *lemaitrei*), or his subgenus *Gambusia.* The latter has five species groups and use of the key would result in the allocation of *G. georgei* to either the *senilis* (six species) or *nobilis* (four species) species groups together more or less equal to the *nobilis* group of Hubbs (1926), Hubbs and Springer (1957), and Rosen and Bailey (1963). Following Rivas, it is possible that *G. georgei* might be closely related to ten species. Nine of these have much longer spines on ray 3 and many free segments on 4a distal to the elbow, all of which are in contrast with the gonopodium of *G. georgei.* The exception is "an

Table 1. Comparison of *Gambusia georgei* and Species Groups of *Gambusia* by Use of Characteristics Extracted from Rosen and Bailey (1963).

Character	Species groups						
	affinis	*nobilis*	*punctata*	*panuco*	*vittata*	*rachowi*	*georgei*
Distal tip of gonopodium	acute to moderately broad	acute	broad	broad	blunt	acute	acute
Ray 3 spines	8–11 short to moderate	6–11 long	10–13 long	12–15 long	poorly formed	6–7 short	8–9 moderate
Longest ray is 3 or 4a	3 or 4a	3	3 or 4a	3	4a	4a	3 or 4a
Distal segments coalesced to elbow	yes	no	no	no	no	no	yes
Elbow relative to 4p serrae	usually distal	opposite or distal	opposite or distal	opposite	no elbow	proximal	opposite
4p serrae	4–7	4–6	4–6	6–8	4–5	4–5	4–5
4p claw	compound with acute tip	simple with acute tip	simple with acute tip	tip curved	tip curved	curved	acute projection
5 claw	J-shaped	J-shaped	arms sub equal	small end	tip curved	acute	J-shaped
Suspensoria	2–3	1–2	3	3	2–3	3	2
No. of gonopodial traits in common with *G. georgei*	7	7	2	1	3	2	

undescribed species, apparently intermediate between *G. heterochir* and *G. sexradiatus,* was recently obtained by me in the Río Tamesí near Ciudad Monte" (Rivas, 1963). The status of this species will be discussed below under *Gambusia myersi* of Rosen and Bailey.

In order to facilitate comparison, we have arranged nine of the diagnostic characters listed by Rosen and Bailey for species groups of *Gambusia* in tabular form. The attributes of *georgei* best match those of the *nobilis* and *affinis* groups (Table 1). It seems to differ from both groups by two characters. The relationship of the length of 3 and 4a as well as the relative position of the serrae and elbow are somewhat questionable because of the variation within groups listed by Rosen and Bailey or variation of the *G. georgei* specimens. The major criteria remaining are the compound nature of the 4p claw (differs from *affinis*) and amount of coalescing in the elbow (differs from *nobilis*).

The elbow of *G. georgei* is well developed and scarcely deviates from that typical for and unique to the *affinis* group. The claw on ray 4p of *G. georgei* is well developed and has a pronounced distal spine. Configuration of the spine is similar to that of the *affinis* group except for the lack of segmentation. We interpret the distal spine to be a fusion of the *affinis*-type compound spine. Relationship of *G. georgei* to the *affinis* group is further supported by the shape of the gonapophyses. The *nobilis* group suspensoria have a pair of posterior projections (uncini) on the first gonapophyses and the anterior end of the second terminates ventrally either by having a long upper arm or a ventral angle to the gonapophyseal shaft. The *affinis* group and *G. georgei* suspensoria (Fig. 2b) have weak or absent uncini on the first gonapophyses and short upper arms and the gonapophyseal shaft more or less parallel to the vertebral column. Most *affinis* group suspensoria have three gonapophyses and most members of *nobilis* group have two. Although this indicates a degree of affinity with *nobilis,* several *affinis* group members have two gonapophyses, notably that species called *G. myersi* by Rosen and Bailey. Since *G. georgei* has attributes of both the *nobilis* and *affinis* groups, this may cause difficulty in species group assignment. This clearly indicates that the species is distinct from all members of both groups in each instance by having those characters that make allocation to that group difficult. That is, *G. georgei* is readily distinguished from all *G. nobilis* species by the fusion of distal 4a segments to the elbow and from the *affinis* group by the simple claw on 4p.

Nevertheless, we have further compared *G. georgei* with several species in both groups to determine to which species *G. georgei* may be closely related. Most likely candidates in the *nobilis* group are *G. atrora* (dorsal colors) or *G. nobilis* (lateral colors) both of which have a rounded claw on 4a. The most likely candidate in the *affinis* group is *G. myersi* of Rosen and Bailey. This species is probably the same as the undescribed member of Rivas' *nobilis* group. "Both" occur in the Río Tamesí near Ciudad Monte and Rivas followed Hubbs (1926) in considering the name *G. myersi* = *G. modesta* as a junior synonym of *G. affinis.* These brightly colored *Gambusia* from the Río Tamesí are not the same as Ahl's types of *G. modesta* (R. R. Miller, pers. comm.) and Rosen and Bailey's description clearly suggests that they are related to *G. affinis* and that their relationship to *G. heterochir* and *G. sexradiata* is remote. The apical spine of ray 4p on Rosen and Bailey's *G. myersi* is relatively short and is scarcely segmented. Furthermore, the Rosen and Bailey *G. myersi* has reasonably long spines on gonapodial ray 3 but the terminal ones are much shorter than those on *G. georgei.* Finally, Rosen and Bailey's *G. myersi* has two gonapophyses, the shape of which are so similar to those of *G. georgei* that we are unable to find consistant differences. Superficially, the color patterns of the two species are quite distinct. Rosen and Bailey's *G. myersi* has an abundance of carotenoid pigments and dark spots. In contrast, *G. georgei* is drab. However, it does have a yellowish background color and a few dark spots that can be interpreted to represent a paled color pattern of the *G. myersi* of Rosen and Bailey. Most noticeable color markings (field identification characters) in *G. georgei* are the dark margins to the dorsal and caudal fins. Comparable areas on Rosen and Bailey's *G. myersi* have faint markings. Both *G. georgei* and Rosen Bailey's *G. myersi* also are sympatric with *G. affinis* (or a sibling species) and one other gambusiine that is primarily a midwater fish—*G. geiseri* and *G. vittata* respectively. Perhaps coincidentally, *G. geiseri* has dark speckling on its fins and *G. vittata* has dark

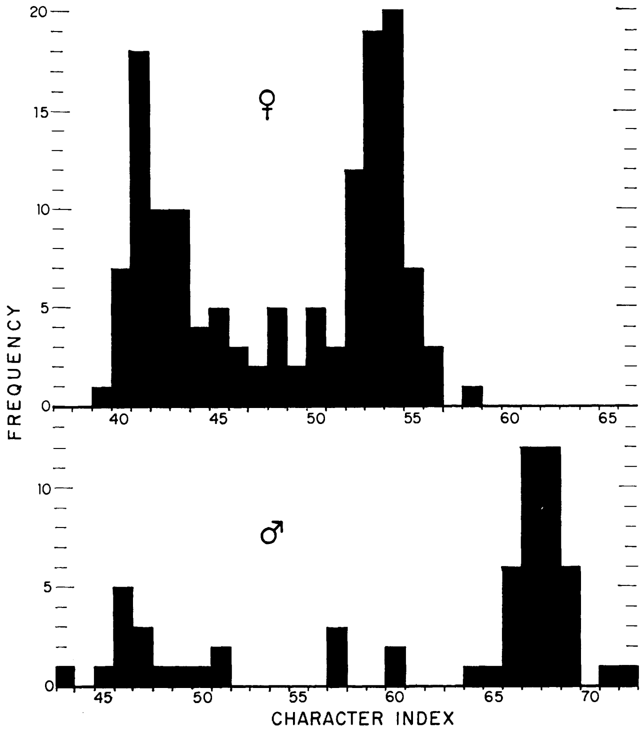

Fig. 3. Bar graphs of coded phenotypic frequencies from female (upper) 25 mm + standard length and mature male (lower) *Gambusia affinis* group, fishes collected with *Gambusia georgei*. Character index derived from adding: head depth at the posterior margin of preopercle/standard length; number of dorsal rays × 4; and the coded figures for color pattern and gonopodial features (Fig. 4).

margins, the reversal of the situation in the sympatric populations of the species here discussed.

We were disturbed about one aspect of the recent discovery of a third species in a limited part of the San Marcos River, because many species are known to have been introduced here (Brown, 1953; Drewry *et al.*, 1958). We examined two female specimens obtained from San Marcos Spring by D. S. Jordan and C. H. Gilbert in 1882 (UMMZ 65250), one has dark caudal margins and seven dorsal rays typical of *G. georgei* and absent or rare in *G. affinis*. Moreover, it was more robust than most *G. affinis* females as are most *G. georgei* females. The other specimen was in poor condition but seems also to represent *G. georgei*. Several gambusiin specimens were collected in the vicinity of the Federal Fish Hatchery in San Marcos between 1925 and 1937. Only one, a hybrid male, provided evidence for the presence of *G. georgei*. Although sampling was minimal, it was apparent that *G. georgei* has been in the San Marcos area for more than 80 years and is likely to be native. Moreover, it has not been found elsewhere. The apparent capture of at least one individual by Jordan and Gilbert indicates that *G. georgei* may have been more common before the area was settled extensively.

Hybridization with *Gambusia affinis*

Although most *affinis*-type individuals in the sympatric area can be easily recognized to species, approximately 10% are intermediate (Figs. 3, 4). We interpret the intermediates to be hybrids. Because males have more distinguishing characters (gonopodial) the distinction of the hybrids from both parental phenotypes is relatively simple. Males of *G. affinis* have character indices between 43 and 51 and those of *G. georgei* between 64 and 72. The five putative male hybrids have 57 or 60 which may be by chance or indicate back crossing with *G. georgei*.

Our preliminary analysis does not permit definitive identification of female hybrids; however, there are more intermediates than

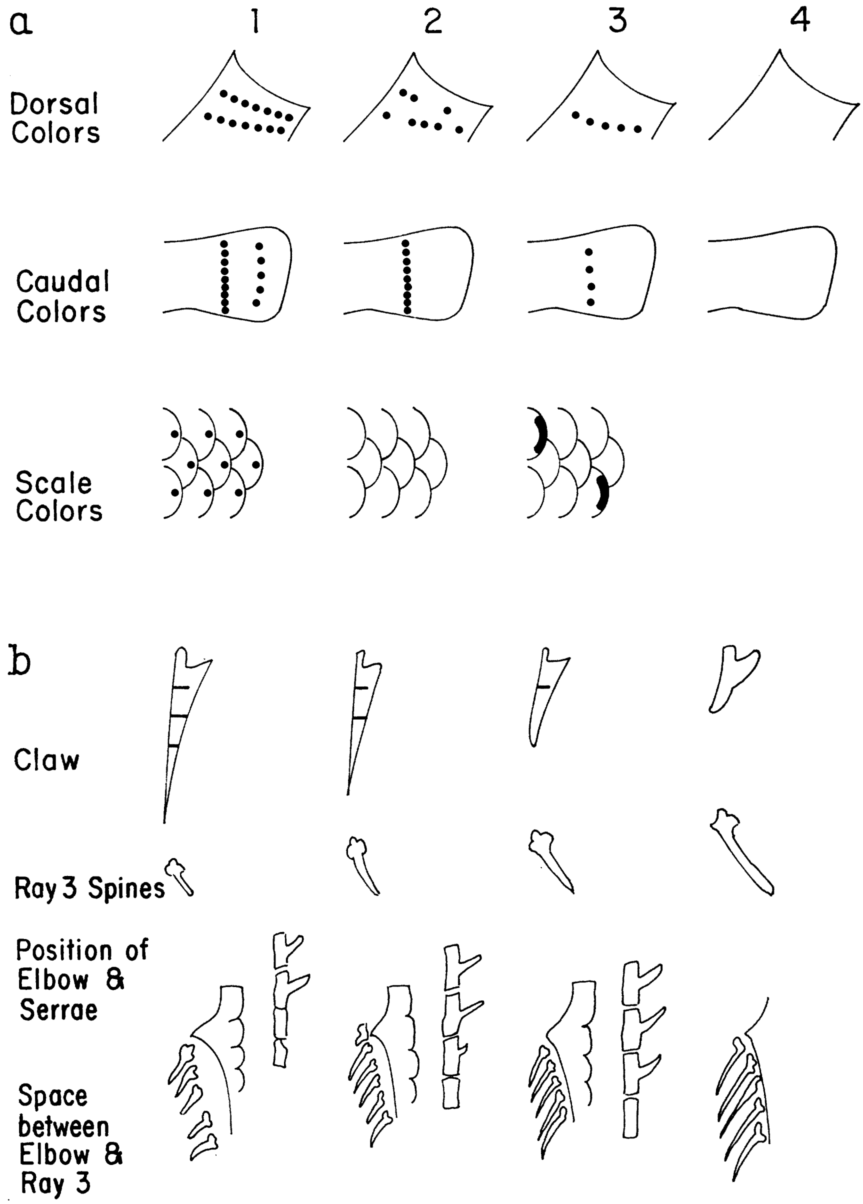

Fig. 4. Codings for character index for colors (a) and gonopodia (b).

would be expected from the interaction of two normal curves. Therefore, a fraction of the females are also hybrids.

Natural hybridization in the sympatric area can be interpreted to signify that the two types are conspecific. More critical analysis, however, reveals that the integrity of each morph is maintained in sympatry despite the potential for introgression. For example, the specimens captured in 1882 seem to be no more distinct than those obtained in 1968 and the 1925 putative hybrid is similar to those obtained 43 years later.

The hybridization evidence can be interpreted phylogenetically in two contradictory ways because ability to hybridize (and morphological similarity) should indicate close phylogenetic relationship and extensive hybridization (introgression) should cause morphologic similarity. Explanation of either must involve considerable circular logic, because the critical support data are not available. It is possible that the morphological similarity to *G. affinis* is caused by past introgression of *G. affinis* chromatin into *G. georgei* resulting in a type of morphologic convergence. If this were correct, the relative uniformity of what we consider to be *G. georgei* would be unlikely because introgression should cause an increase in variance. In contrast, the potential to hybridize with *G. affinis* can be interpreted to reflect close relationship to *G. affinis*. If *G. georgei* is not a member of the *affinis* group, it belongs to the *nobilis* group to which the sympatric *G. geiseri* belongs. If *georgei* and *geiseri* were closely related, it would be expected that they would hybridize with each other rather than would either with *affinis*. Sympatry of *nobilis* group species occurs only in the Balmorhea area where *nobilis* and *geiseri* may be found together with *affinis*. Hybrids do occur but they are all between *nobilis* and *geiseri* (Peden, MS). Moreover, in artificial pools, hybridization has been noted between *hurtadoi* and *heterochir*, two other members of the *nobilis* group. Despite extensive sympatry, intergroup hybridization is localized. Therefore, we feel that the overall hybridization evidence favors placing *georgei* in the *affinis* group.

Ecology

Because the sympatric occurrence of three gambusiins is rare, we have examined the ecology with care. *G. geiseri* is the most distinct species morphologically and ecologically. It predominates away from the stream bank, often occurring in midwater. Schools of *G. geiseri* are usually near or in the middle of dense vegetation and often abound in rapid but not turbulent water. Neither *G. affinis* nor *G. georgei* occur abundantly far from the stream bank or in moderate current. *G. affinis* is well known for its wide distribution and its ecology in San Marcos River reflects that circumstance. It is abundant in all small tributaries that have relatively large thermal fluctuations. It also is abundant downstream in the San Marcos River where the unique thermal consistency ±0.25° C (Brown, 1953) is altered by seasonal conditions. *G. affinis* predominates in the shallow edges with dense vegetation and *G. georgei* is essentially restricted to the shallow areas without dense aquatic vegetation in the main San Marcos where thermal conditions vary little. These mud bottomed areas are rare in the 2 km of the San Marcos River that maintains thermal consistancy. As a consequence, we estimate that there are fewer than 1000 individuals in the San Marcos River at any given time. They are most common under bridges where shade inhibits vegetation. A slight alteration of the river channel could easily exterminate *G. georgei*.

Acknowledgments

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