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Origin of the Characid Fish Genus *Bramocharax* and a Description of a Second, More Primitive, Species in Guatemala

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ABSTRACT

A new species of the characid fish genus *Bramocharax* is described from a karst region along the northern foothills of the Sierra de Chamá in Guatemala. The region is characterized by sinks and caverns into which streams of various sizes disappear. The points of emergence or hydrographic relationships of these streams are not always evident, but the ichthyofaunal evidence presented helps to tie some of them to two of the major tributaries of the Río Usumacinta system. The phyletic relationships of the three presently known forms of *Bramocharax* (the species being described here and the two subspecies of *bransfordi*) are analyzed. The zoogeographic inferences drawn from the proposed phylogeny are that the genus *Bramocharax* arose in the Río Usumacinta system and then spread southward to the Río San Juan system of Nicaragua and Costa Rica. The populations of *Bramocharax* inhabiting lakes Nicaragua and Managua are identified as historically the most recently established.

INTRODUCTION

Continued exploration in the mountainous karst region of Alta Verapaz, Guatemala, has revealed the existence of additional endemic fishes in isolated river basins of the Río Usumacinta system. This region, along the northern foothills of the Sierra de Chamá, is typical karst topography of

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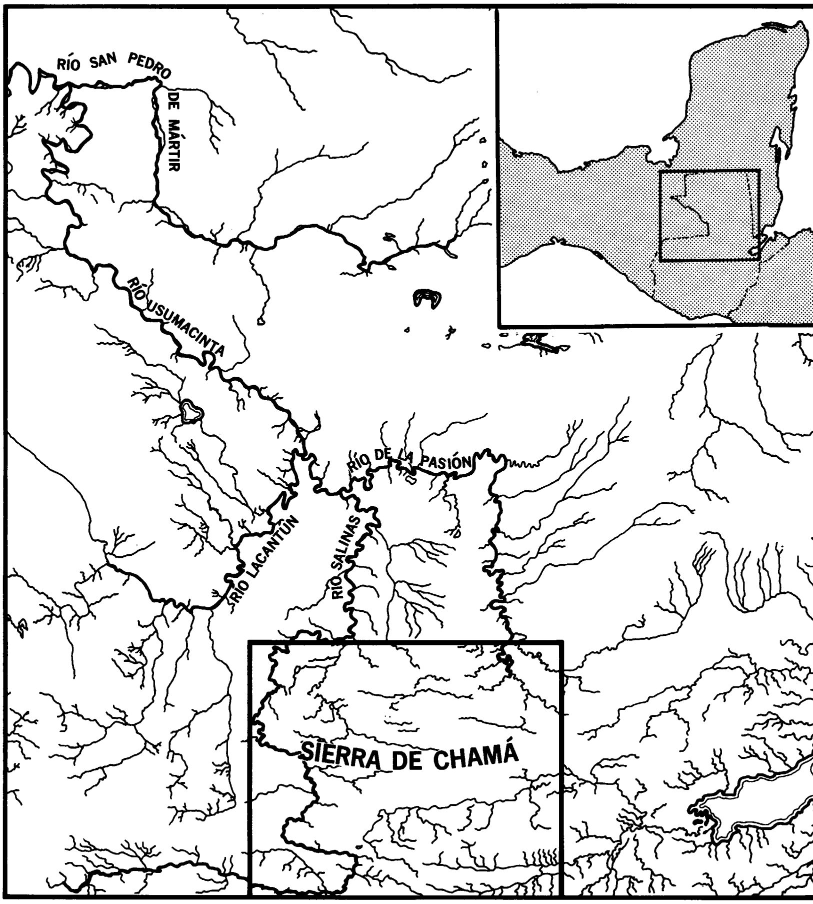

FIG. 1. Four main tributaries of the Río Usumacinta in Guatemala and Mexico. This report is concerned with the karst region of the Sierra de Chamá, shown in box at bottom of map and enlarged in same section of figure 2. The inset (upper right) of southern Mexico and northern Central America shows the entire region covered in this map section.

sinks, caverns, and valleys with unsystematic drainage patterns and disappearing streams. At present five such streams or rivers with subterranean drainage have been explored by Reeve M. Bailey and me, although there are many more that have been recorded on recent topographic maps and viewed during our aerial surveys. Collecting has thus far been concentrated in isolated basins associated with the headwaters of two of the main branches of the Usumacinta, the Río de la Pasión and the more westerly

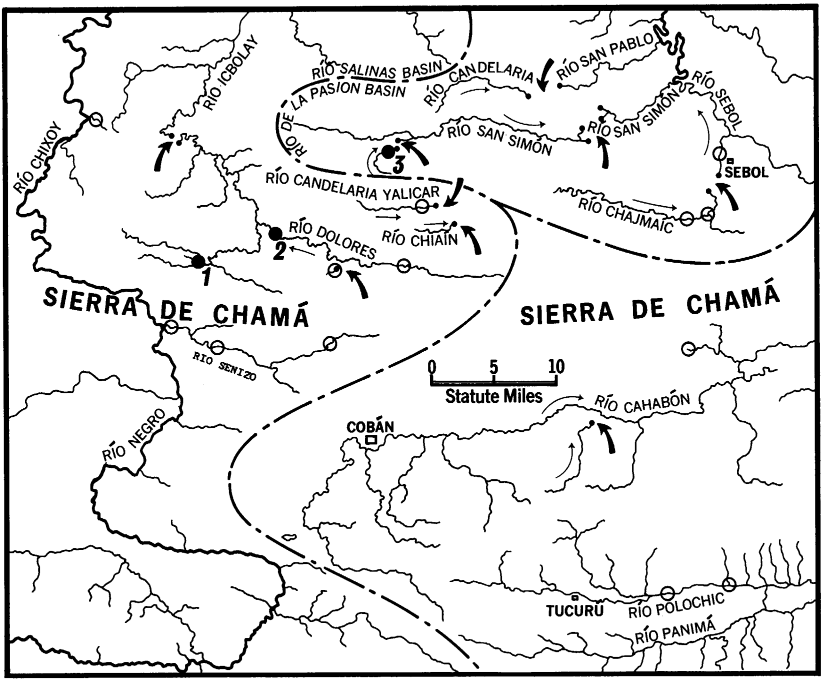

FIG. 2. Karst region of Alta Verapaz, Guatemala, along foothills of Sierra de Chamá. See figure 1. Rivers and streams belonging to different hydrographic basins are set off by boundary lines of long and short dashes. To the west *left* is the Río Salinas Basin. Northeastern basin *top right* is the Río de la Pasión. At the *lower right* are main branches of Río Polochic Basin. Heavy arrows point to subterranean channels, sinks, or caverns associated with major disappearing streams of this region. Slender arrows near watercourses show direction of current. Closed and open circles are sites from which fish were collected during 1963, 1968, and 1971. Closed circles, numbered 1, 2, and 3, are localities from which *Bramocharax baileyi* was collected.

Río Salinas (fig. 1). Until 1971, *Bramocharax* was twice collected in the Río Chajmaíc (with an underground connection to the Río de la Pasión) and once in the Río Dolores (with an underground connection to the Río Salinas). The only two, small, apparently juvenile specimens taken in the Río Dolores were regarded as representatives of a disjunct population of the recently described *Bramocharax bransfordi dorioni* Rosen (1970), which was otherwise based on the several hundred specimens from the Río Chajmaíc Basin. Additional collecting during March, 1971, in the general area of the Río Dolores, to the west of Chajmaíc, yielded two more samples of *Bramocharax*, totaling 11 specimens. All 11 appear to represent a single form and are inseparable from the original two specimens caught earlier in the Río Dolores. Study of these 13 individuals has shown them to be distinct in body proportion, pigmentation, and dentition from members of the Río Chajmaíc population, and they are described herewith.

The field work for this and related studies of Guatemalan fishes is supported by funds from Mr. James C. Greenway, Jr.

Bramocharax baileyi, NEW SPECIES

Figures 1–6; tables 1, 2

Bramocharax bransfordi dorioni ROSEN, 1970 p. 3 (specimens 33.5 and 66.5 mm. standard length [erroneously given as 24, rather than 34, and 66 mm.] from the Río Dolores [AMNH[1] 29415]).

MATERIAL: The holotype (AMNH 30197) is a subadult 68.5 mm. in standard length, obtained with rotenone in an isolated basin, the Río San Simon, 6 km. due west of Chisèc, Alta Verapaz, Guatemala, March 6, 1971, by R. M. Bailey, D. E. Rosen, and party. Taken with the holotype were a subadult 63.5 mm. and a juvenile 35.5 mm. in standard length (AMNH 30198). Additional specimens were secured with rotenone in 1968 and 1971 in Alta Verapaz by R. M. Bailey and D. E. Rosen, as follows: 1968, 2 specimens (AMNH 29415) 33.5 and 66.5 mm. in standard length in the Río Dolores, along the shore, at Yaxcabnal, March 21; 1971, 8 specimens (AMNH 30199) 31.1 to 64.8 mm. in standard length in an outlet tributary of a lagunetta between the Río Rociá Pemech and the Río Canillá due west of Finca Taqueç Canguinic, March 23. The 1968 locality was reached by light plane and the two 1971 sites by helicopter.

DIAGNOSIS: A slender bodied, long-snouted form of *Bramocharax* (depth 3.2–3.8 in standard length; snout 26 to 29 percent of head length) with the humeral spot vertical, extending below lateral line; outer premaxillary teeth well-developed, perforating upper lip, and separated from the inner teeth in a distinct row of four evenly spaced teeth or the anterior three teeth well separated from the fourth; the premaxillary canines (of the inner tooth row) only slightly larger than succeeding teeth and fitting within sockets in the lower jaw when the mouth is closed; second tooth of mandible only slightly smaller than first and third; diastemas between second and third, and third and fourth mandibular teeth slight or absent; all enlarged mandibular and maxillary teeth and all inner premaxillary teeth notably cuspidate, with as many as six lateral cusps.

DESCRIPTION: Dorsal fin rays, 11 (13); anal fin rays, 25 (1), 26 (3), 27 (6),

[1] AMNH, the American Museum of Natural History.

28 (3); pelvic fin rays (sum of right and left counts), 16 (13); pectoral fin rays (sum of right and left counts), 25 (1), 28 (4), 29 (3), 30 (4), 32 (1); lateral line scales, 36 (1), 37 (9); scale rows on left side (counted obliquely backward from pelvic fin origin), 14½ (7), 15½ (5). Proportional measurements that distinguish *baileyi* are given in figure 5 and table 1. As with *Bramocharax bransfordi bransfordi* Gill and *B. b. dorioni* a ratio of snout to head length plotted against standard length provides the simplest morphometric separation of *baileyi*. Measurements of greatest depth of body in relation to standard length show that *baileyi* is consistently slender bodied, comparable with relative depth measurements of adult male *bransfordi bransfordi* (standard length divided by greatest depth in *baileyi*: 3.2 to 3.8; in male *bransfordi bransfordi*: 3.4 to 3.5). Young and adult females of *bransfordi bransfordi* have values comparable with those of young and adult males and females of *bransfordi dorioni*: 2.7 to 3.3. In life, the body color of *baileyi* is silvery with a pale yellow or yellow-green cast. The pelvic, anal, and caudal fins are a pale rosy color, and the dorsal is pale yellow-orange. The distinguishing humeral blotch has a ventral vertical component that extends below the lateral line. Melanophore patterns are shown in figures 3 and 4.

Dentitional characters are discussed at length below.

GEOGRAPHY: The first known sample of *baileyi* was taken in the Río Dolores, along the shore at the village of Yaxcabnal (fig. 2, loc. 2). Specimens collected subsequently are from a surface tributary to the Río Dolores (a small stream between the Río Rociá Pemech and the Río Canillá; fig. 2, loc. 1) and from a disappearing stream section of the Río San Simón (fig. 2, loc. 3). The latter collection is especially interesting because the Río San Simón is shown on recent topographic maps of the region (part of a series produced by the Dirección General de Cartagrafía, República Guatemala) to drain into the upper Río de la Pasión, whereas the other two localities are hydrographically part of the Río Salinas (Río Chixoy-Río Negro) Basin. The topographic sheets show two separate disappearing stream sections of the Río San Simón. The first of these, from which *baileyi* was collected, is about 4 miles long and passes under a low ridge to the north to join the second and larger disappearing stream section. The latter is about 30 miles long and flows to the east where it divides into two subterranean passages at the foot of a NW-SE ridge. It emerges to the east of this ridge as two streams that join and flow directly into the upper Río de la Pasión (Río Sebol). That the first two and the third collecting stations are in different hydrographic basins is suggested by some of the faunal associates of *baileyi* in the two regions. In the two collections in the Río Dolores Basin *baileyi* is associated with the same as yet unde-

TABLE 1

Morphometric and Meristic Features of *Bramocharax baileyi*

(Measurements are in Millimeters)

	St.L.	G.D.	St.L./G.D.	H.L.	Sn.L.	Sn.L./H.L. ×1000	DFR	AFR	P_1R R+L	P_2R R+L	LL.Sc.	Sc.R.
Río San Simón												
AMNH 30197	68.5	20.0	3.4	22.2	6.1	275	11	28	29	16	37	14½
(Holotype)												
AMNH 30198	63.5	19.6	3.2	21.2	6.0	283	11	27	28	16	37	14½
	35.5	11.1	3.2	11.7	3.1	265	11	27	28	16	37	14½
Río Dolores, Yaxcabnal												
AMNH 29415	66.5	17.7	3.8	21.2	6.1	288	11	27	30	16	36	15½
	33.5	9.5	3.5	11.3	3.1	274	11	27	28	16	—	15½
Stream between Río Rociá Pemech and Río Canillá												
AMNH 30199	64.8	19.2	3.4	21.0	5.6	267	11	27	30	16	37	14½
	64.2	19.6	3.3	20.2	5.5	272	11	26	32	16	37	14½
	63.9	17.5	3.6	21.5	6.0	279	11	27	30	16	37	15½
	58.5	17.0	3.4	19.1	5.2	272	11	28	28	16	37	14½
	40.6	12.7	3.2	13.4	3.7	276	11	26	25	16	37	15½
	39.3	11.4	3.4	12.6	3.5	278	11	28	30	16	37	14½
	38.4	10.8	3.5	13.0	3.4	261	11	25	29	16	—	—
	31.1	9.0	3.4	11.0	2.9	264	11	26	29	16	—	15½
Mean			3.4			273	11	26.8	28.9	16	36.9	14.9
Standard Error			±0.01			±0.14	±0.0	±0.22	±0.76	±0.0	±0.03	±0.07

Abbreviations: St.L., standard length (snout tip to caudal base); G.D., greatest depth of body; H.L., head length (snout tip to edge of opercular membrane); Sn.L., snout length (snout tip to orbital rim); DFR, dorsal fin rays (all rays with separate bases); AFR, anal fin rays (all rays with separate bases); P_1R, R+L, pectoral fin rays (right plus left); P_2R, R+L, pelvic fin rays (right plus left; splint not counted); LL.Sc., lateral line scales; Sc.R., scale rows (counted obliquely backward from two scale rows in front of dorsal fin origin).

A snout length/head length index of 275 may also be expressed as a snout length that is 27.5 per cent of head length.

scribed forms of the poeciliid genera *Xiphophorus* and *Heterandria*. It also occurs in the small stream between the Río Rociá Pemech and Río Canillá with the recently described *Scolichthys greenwayi* Rosen; *S. greenwayi* is otherwise known both from the Río Dolores Basin at Cubilguitz and in an upper tributary to the Río Senizo that flows directly into the upper Río Salinas (Río Negro). In the Río San Simón, *baileyi* was taken together with *Xiphophorus helleri guentheri* Jordan and Evermann and *Heterandria bimaculata* (Heckel), both widespread forms that are in all the main branches of the Río Usumacinta system exclusive of the Río Dolores. Although *Xiphophorus helleri guentheri* is not known from other isolated karst valleys of this region of Alta Verapaz, *Heterandria bimaculata* is abundant in the isolated Río Chajmaíc that drains into the upper Río de la Pasión. Between the Río San Simón and the Río Dolores Basin there is a small oval valley with one major disappearing stream, the Río Candelaria Yalicar, and two smaller, possibly intermittent ones. The Río Candelaria Yalicar contains, among other fishes, forms of *Xiphophorus* and *Scolichthys* that are characteristic of the Río Dolores, although the *Heterandria* there is distinct from all others. *Bramocharax baileyi* does not occur in that area, however. The Río Candelaria Yalicar Valley is equidistant between the Río Dolores and the Río San Simón, about 4 miles from each, and shares some of the unique karst region faunal components only with the Río Dolores. We may therefore tentatively accept the hydrographic interpretation of the Río San Simón as a stream historically distinct from the Río Salinas and probably related to the Río de la Pasión Basin. If this interpretation is sustained by future work then it is evident that *Bramocharax baileyi*, at one time, may have been widespread in the two main tributaries of the Río Usumacinta, or that latterly *baileyi* has transferred from one basin to the other, and that it owes its survival in the upper reaches of the Río de la Pasión and Río Salinas systems to the development of the topographically isolated refugia that characterize this karst region. The evident possibility also exists that *Bramocharax baileyi* was at one time sympatric with *Bramocharax bransfordi dorioni* in the upper Río de la Pasión. *Bramocharax bransfordi dorioni* is presently known only from the isolated, intermontane Río Chajmaíc, but the Río Chajmaíc is now separated from the lower Río San Simón by about 10 airline miles and from the upper Río San Simón by half that distance.

A more comprehensive report on the karst fauna of Guatemala is presented in a forthcoming article.

ETYMOLOGY: This new form is named for Dr. Reeve M. Bailey: teacher, friend, and colleague of 26 years, and field companion in Guatemala during 1966, 1968, and 1971.

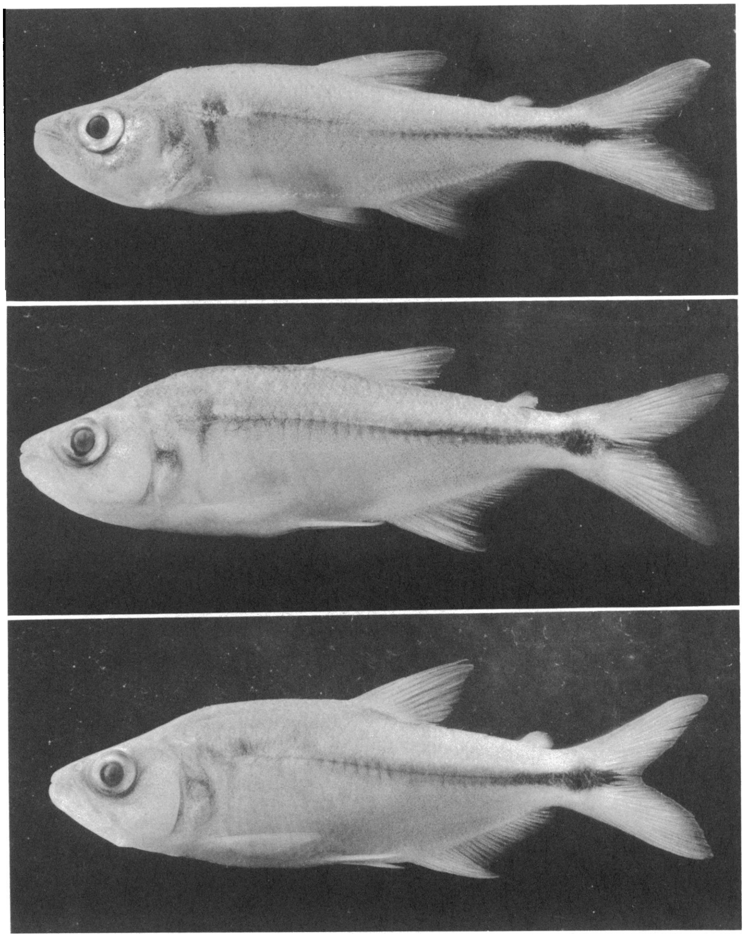

FIG. 3. Guatemalan forms of *Bramocharax*. *Top*: *Bramocharax baileyi*, paratype, AMNH 30199, 63.9 mm. standard length. *Center*: *Bramocharax baileyi*, holotype, AMNH 30197, 68.5 mm. standard length. *Bottom*: *Bramocharax bransfordi dorioni*, AMNH 29412, 73 mm. standard length.

TAXONOMY AND COMPARISONS: Preliminary comparisons of *Bramocharax baileyi* with *Bramocharax bransfordi dorioni* Rosen suggested a close relationship between them, and indeed the first two specimens of *baileyi* collected in 1968 were not separated as a distinct taxon. So striking are the superficial resemblances between *baileyi* and *b. dorioni*, that early in the present investigation it was thought best to treat the two as subspecies of a single form distinct from *bransfordi bransfordi* in which, alone among the three

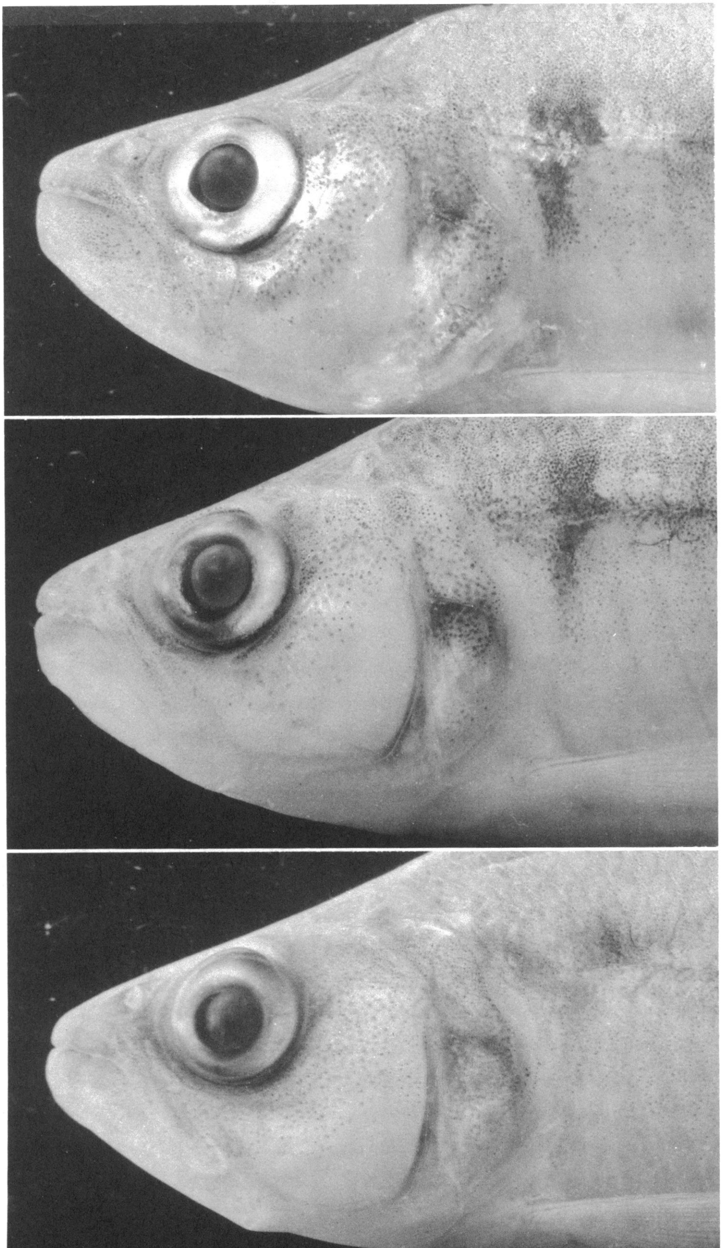

FIG. 4. Guatemalan forms of *Bramocharax*, anterior third of body, to show details of head and humeral spot. Specimens as in figure 3. *Top*: *B. baileyi*, paratype. *Center*: holotype. *Bottom*: *B. bransfordi dorioni*.

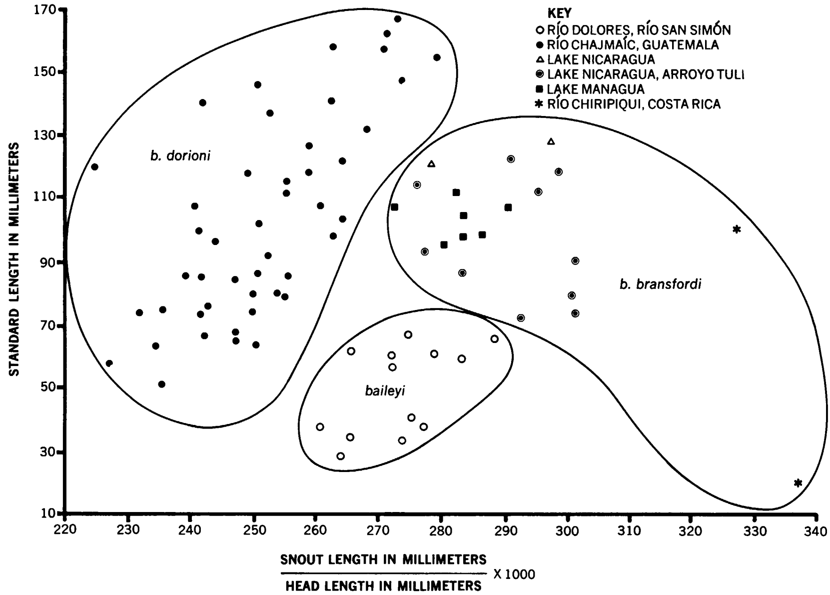

FIG. 5. Snout length/head length indexes in populations of *Bramocharax*. Note that *baileyi* tends to approach *b. dorioni* at smaller sizes and *b. bransfordi* at larger sizes, although smallest individuals of each taxon are readily separated.

members of this group, the upper canines lie exposed along the outside of the lower lip when the mouth is closed. Such an interpretation of relationships seemed also to accord well with their geographic relationships: *baileyi* and *b. dorioni* in nearby rivers of the same drainage basin (Río Usumacinta) and *b. bransfordi* isolated far to the south in the Río San Juan system and the great lakes of Nicaragua. Subsequent detailed comparisons of the morphometric, pigmentary, and dentitional characteristics in the three populations of *Bramocharax* and in similar and related characids such as *Astyanax* showed that these early interpretations were without foundation. In relative snout length *baileyi* is intermediate between *b. dorioni* and *b. bransfordi* (fig. 5), and in five of six diagnostic dentitional features *b. dorioni* and *b. bransfordi* are similar, but distinct from *baileyi* (table 2). Likewise in the single diagnostic pigmentary feature *b. dorioni* resembles large *b. bransfordi* which also has the humeral spot well developed only above the lateral line. Smaller *b. bransfordi*, including some adult males, have a strong ventral extension of the humeral spot below the lateral line, as in *baileyi*. All the known *baileyi* are small, however, and a test of the taxonomic utility of this pigmentary trait must await the collection of

TABLE 2

PRIMITIVE CHARACTERS AND DERIVED CHARACTERS (IN PARENTHESES) IN *Bramocharax bransfordi bransfordi*, *B. bransfordi dorioni*, AND *B. baileyi*, WITH A COMPARISON OF OTHER NEW WORLD CHARACID GENERA

bransfordi bransfordi	*bransfordi dorioni*
(Snout much longer than eye)	Snout and eye subequal
(Upper canines overlying lower lip)	Upper canines concealed
(Inner premaxillary and mandibular teeth separated by large diastemas)	(Inner premaxillary and mandibular teeth separated by large diastemas)
(Premaxillary and mandibular teeth slightly or not at all cuspidate)	(Premaxillary and mandibular teeth slightly or not at all cuspidate)
(Second mandibular tooth notably smaller than first and third)	(Second mandibular tooth notably smaller than first and third)
(Outer premaxillary teeth reduced and closely aligned with inner teeth; covered by upper lip)	(Outer premaxillary teeth reduced and closely aligned with inner teeth; covered by upper lip)
(Humeral spot diffuse, well developed above lateral line in most individuals)	(Humeral spot diffuse, well developed above lateral line only)
baileyi	OTHER TETRAGONOPTERINE GENERA
(Snout slightly longer than eye)	Snout subequal to, or smaller than, eye in most
Upper canines concealed	Upper canines, when present, concealed
Inner premaxillary and mandibular teeth with small or no diastemas	Teeth in principal tooth rows not separated by diastemas
Premaxillary and mandibular teeth notably cuspidate	Premaxillary and mandibular teeth notably cuspidate in most
Second mandibular tooth only slightly smaller than first and third	Second mandibular tooth equal in size to, or only slightly smaller than, the first and third
Outer premaxillary teeth well developed and well separated from inner teeth; perforating upper lip	Outer premaxillary teeth well developed, separated from inner teeth, and perforating the upper lip in most
Humeral spot with a strong vertical component below lateral line	Humeral spot with vertical component below lateral line in many species of *Astyanax* (incl. *A. fasciatus*), and in *Moenkhausia*, *Gymnocorymbus*, *Hemigrammus*, *Hyphessobrycon*, *Deuterodon*, *Creagrutus*, *Bryconamericus*, *Glandulocauda*, *Hemibrycon*

larger individuals. In fact, *b. dorioni* and *baileyi* exactly resemble each other only in having the upper canines concealed, rather than overhanging the lower lip, when the mouth is closed. A comparison of the eight traits analyzed in table 2 with these same attributes in *Astyanax* shows, further, that *baileyi* is more similar in some dentitional and pigmentary characters to *Astyanax* than it is to the other two forms of *Bramocharax* (figs. 6–9).

Specifically in *Bramocharax baileyi* and in various Guatemalan examples of *Astyanax* the upper canines are concealed, the inner premaxillary and mandibular teeth have small or no diastemas between them, the premaxillary and mandibular teeth are notably cuspidate, the outer premaxillary teeth are well developed, perforate the upper lip, and are well separated from the teeth of the inner series, and the second mandibular tooth is only slightly smaller than the first and third. Apart from the concealment of the upper canines—an arrangement common to most characids—the dentitional similarities of *baileyi* and *Astyanax* occur also in various other genera of New World characids. For example, having the second mandibular tooth smaller—but not much—than the first and third is characteristic also of *Bryconamericus*, *Argopleura*, and *Hemibrycon*. Having upper canines—but not notably enlarged ones—is common also to *Hemigrammus*, *Hyphessobrycon*, *Thayeria*, *Bryconamericus*, and *Hemibrycon*. *Bramocharax baileyi*, the species of *Astyanax*, and those of numerous other genera, have the outer series of premaxillary teeth well separated from the inner series. The single distinguishing pigmentary feature of *baileyi*, a humeral spot with a ventral vertical component that extends below the lateral line, also is widespread among New World characids, including many forms of *Astyanax*, and is possibly also primitive with respect to the condition of the spot in *b. dorioni* and *b. bransfordi*. It appears, then, that many of the features in which *baileyi* is distinguished from *b. dorioni* and *b. bransfordi*, but not from various other groups of characids, may be primitive features of the group called the Tetragonopterinae by Eigenmann (1917-1927) and Eigenmann and Myers (1929). Conversely, the dentitional and pigmentary characters that align *b. dorioni* and *b. bransfordi* seem to represent derived character states with respect to New World characids.

Two questions are raised: On what evidence is *baileyi* included in the nominal genus *Bramocharax*, and on what grounds, if any, can the genus *Bramocharax* be retained as a useful and phyletically meaningful taxon?

Initial comparison of the forms of *Bramocharax* and *Astyanax* suggests that *Bramocharax* is immediately distinguished by its longer snout, longer and more consistently concave anterodorsal profile, and longer head. In apparent snout length *Astyanax* is enormously variable for a number of reasons, which include actual differences in snout length in relation to standard length, snout length in relation to head length, and in relation to orbital diameter. Head length and eye size also vary greatly, even within a single population or between contiguous populations (fig. 11). Comparisons of snout length and orbit size will not, therefore, separate all individuals of *Bramocharax* and *Astyanax*, for the relative proportions of snout and eye in relation to head length are about the same in both.

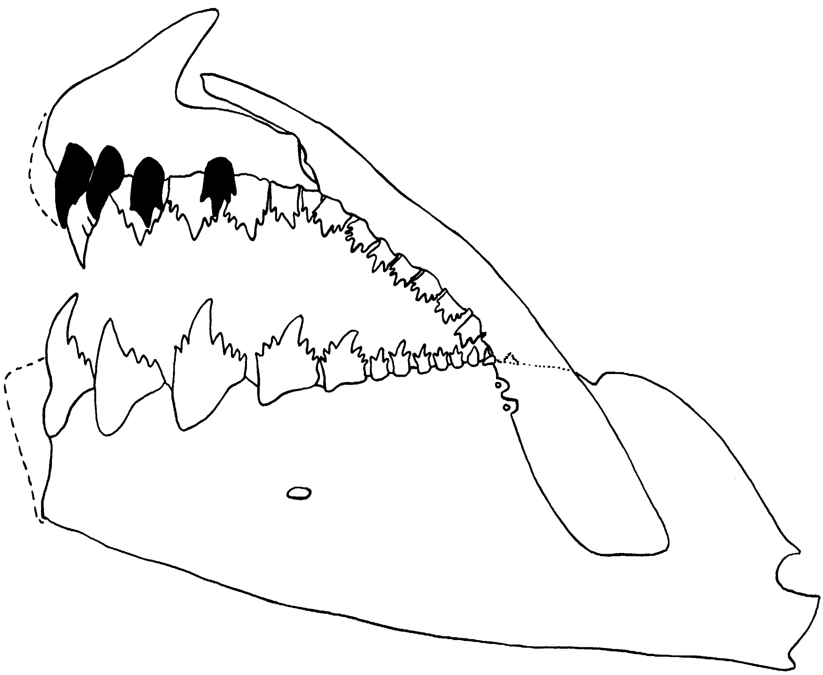

FIG. 6. Upper and lower jaw teeth in *Bramocharax baileyi* of 64.8 mm. standard length, AMNH 30199. Outer premaxillary teeth in solid black.

The two groups are generally separable, however, in regard to relative head length, which in *Bramocharax* is 30 to 33 percent of standard length and in *Astyanax*, only about 25 percent of standard length. In dentition *Bramocharax bransfordi bransfordi* and *B. b. dorioni* are clearly differentiated from *Astyanax* in the reduction and grouping of the outer premaxillary teeth, in the close alignment of the outer and inner series of premaxillary teeth, in the height of the lower canines, the relative smallness of the second tooth in the mandibular series, the diastemas between the mandibular teeth, in the reduction in number and size of lateral tooth cusps, and in the large number of maxillary teeth (as many as 19) that can develop in large individuals. These differences, except for number of lateral tooth cusps and number of maxillary teeth, are consistent even in comparisons of the smallest individuals. In contrast, *Bramocharax baileyi* is more difficult to separate from *Astyanax* in dentitional characteristics and part of the difficulty may be related to the relatively small size of the presently known examples of *baileyi*. The largest number of well-developed maxillary teeth

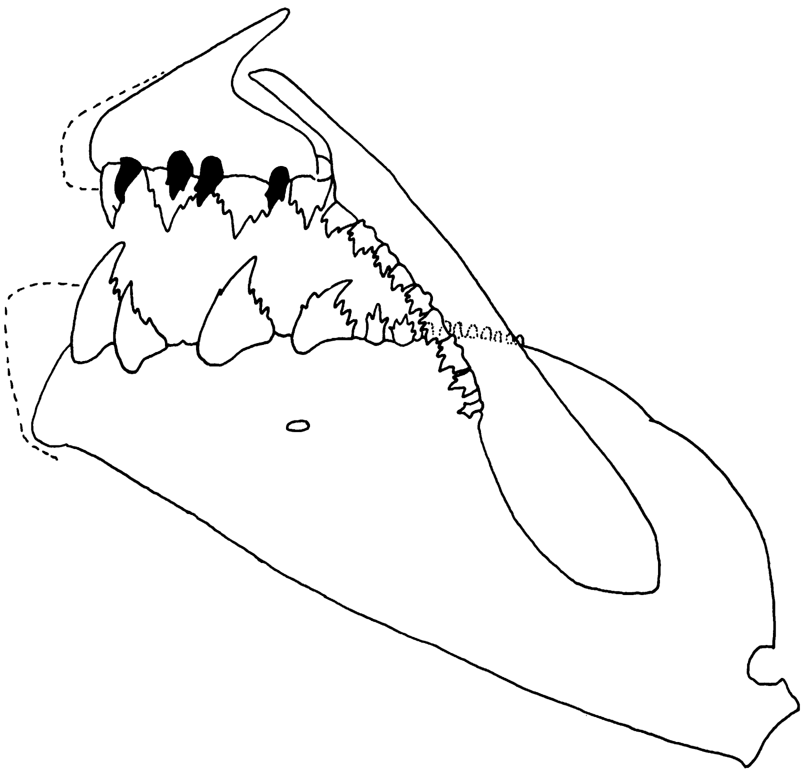

FIG. 7. Upper and lower jaw teeth in *Bramocharax bransfordi dorioni* of 66 mm. standard length, AMNH 29412. Outer premaxillary teeth in solid black.

known in *baileyi* is seven, although one specimen (fig. 6) shows evidence of incipient development of three additional teeth. Eigenmann (1921) recorded as many as nine maxillary teeth in *Astyanax nicaraguensis* Eigenmann and Ogle, and not uncommonly five to seven in various species of the subgenus *Astyanax*. When and if larger examples of *baileyi* are collected, lateral cusp reduction and an increased maxillary dentition may be found to typify this form also. Nevertheless, *baileyi* is at present distinguished in dentition from the forms of *Astyanax* only by the slightly enlarged mandibular canines and by the presence in five of the seven largest of the 13 known individuals of small diastemas between the second and third and between the third and fourth mandibular teeth (compare figs. 6 and 9). These two rather slight differences in dentition between *baileyi* and *Astyanax* are the same dentitional traits that support the inclusion of *baileyi* in *Bramocharax*, but, at the same time, demonstrate that it is the

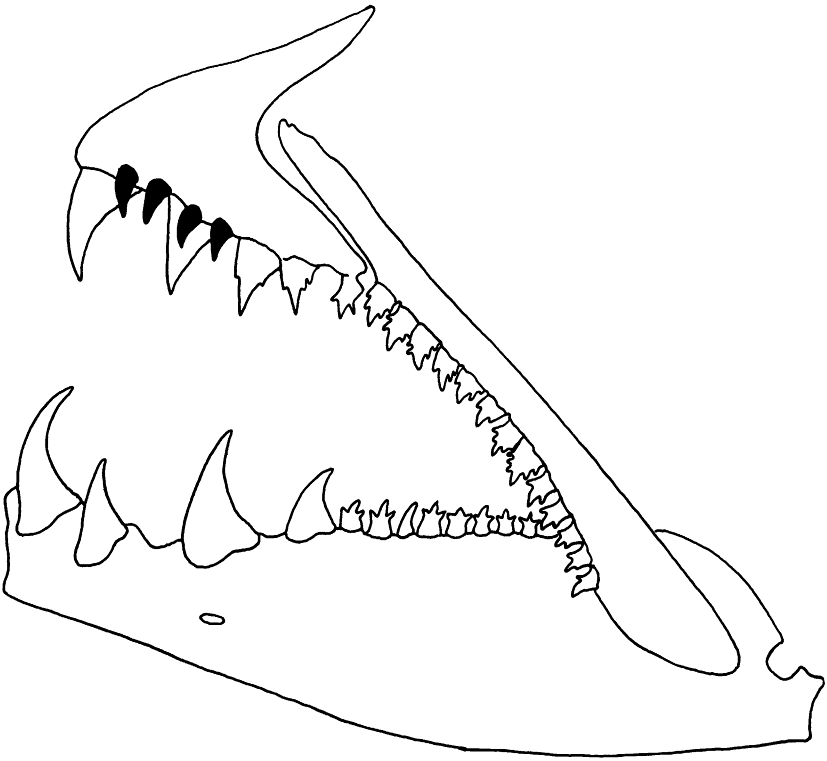

FIG. 8. Upper and lower jaw teeth in *Bramocharax bransfordi bransfordi* of 98.5 mm. standard length. Outer premaxillary teeth in solid black.

proportional elongation of the head and its parts (see, for example, mandibular shape in figs. 6–10) that primarily distinguishes *Bramocharax* from *Astyanax*. It is tempting to hypothesize that existing dentitional differences between the two are directly the result of differences in jaw length, i.e., that as the jaw elongates the outer premaxillary teeth are reduced and are aligned with the inner series, the number of maxillary teeth increases (corresponding to an increase in maxillary length?), and that diastemas develop between the teeth of the main tooth rows. No such simple relationships are suggested, however, by comparison of the long-headed, long-snouted *Astyanax nasutus* Meek with the shorter headed and shorter snouted *Astyanax fasciatus* (Cuvier) (figs. 9, 10, 12). Moreover, *Bramocharax baileyi*, which has a relatively longer snout in relation to head length than *b. dorioni* (fig. 5), should, according to this hypothesis, also have smaller outer premaxillary teeth aligned more like those of *b.*

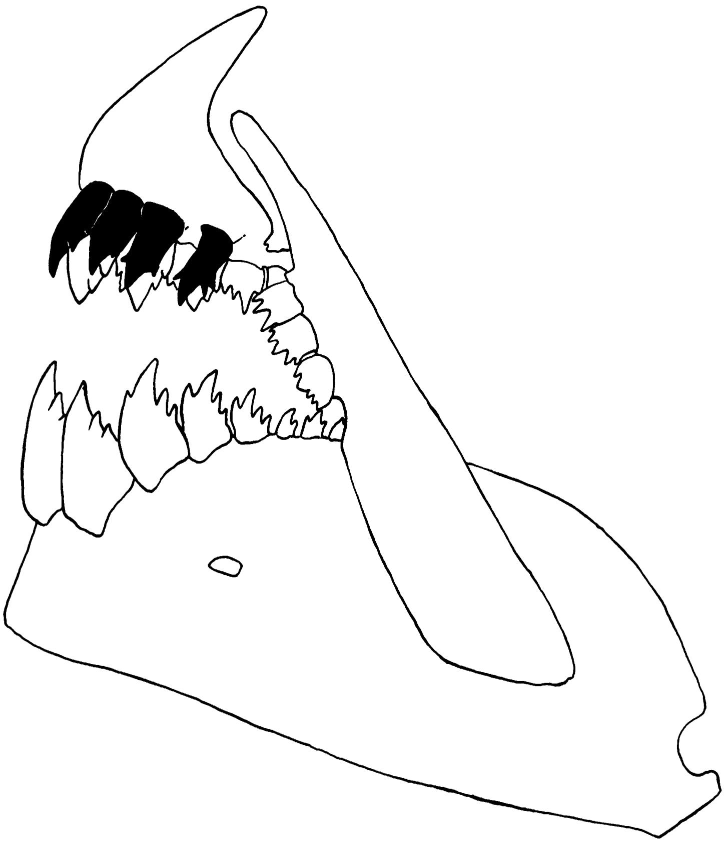

FIG. 9. Upper and lower jaw teeth in *Astyanax fasciatus* of 65 mm. standard length, AMNH 30163, taken together with *Bramocharax baileyi* in the Río San Simón. Outer premaxillary teeth in solid black.

bransfordi, and should have larger diastemas among the teeth of the principal tooth rows than does *b. dorioni*. The reverse is true, and the distribution of outer premaxillary teeth follows as *Astyanax* pattern in *baileyi* and a *b. bransfordi* pattern in *b. dorioni*. It is therefore evident that tooth size may be independent of tooth pattern and that both may be independent of jaw length. This conclusion tends to reinforce the significance of dentitional traits in the species of *Bramocharax* as evidence of the phyletic unity of the three forms. A corollary conclusion is that the genus *Bramocharax* should be maintained, at least until there is a thorough review of all the rather similar and generalized New World tetragonopterines.[1]

[1] Another New World characid, *Scissor macrocephalus* Günther (see Eigenmann and Myers, 1929, pp. 453–454, pl. 64, fig. 7), is very similar in body proportions to the

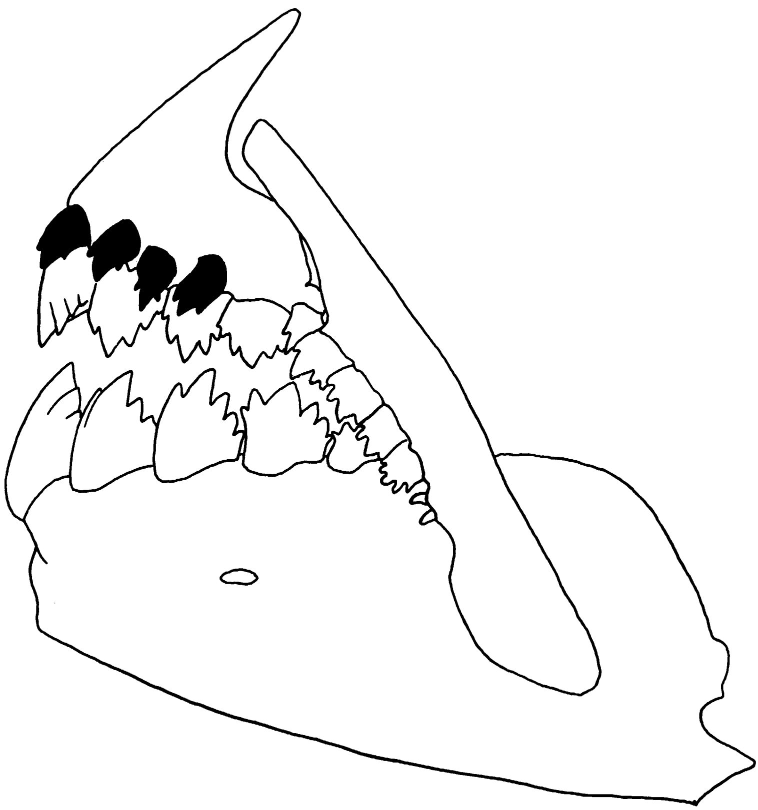

FIG. 10. Upper and lower jaw teeth in *Astyanax nasutus*. Composite made from paratypes (Field Museum of Natural History 5908) 69 mm. to 78 mm. standard length. Outer premaxillary teeth in solid black.

species of *Bramocharax*. *Scissor macrocephalus* is known only from the holotype, and its place of origin, although not certainly known, was believed by Günther to be Surinam. It is like *Bramocharax* also in meristic details; counts made from the holotype (British Museum [Natural History] 1858.6.14.1) are: dorsal rays, 11; anal rays, iii-26; pectoral rays (right + left), 13 + 15; pelvic rays (right + left), 8 + 9; lateral line scales, 37 (Eigenmann and Myers, *loc. cit.*, gave 38). In the proportions of snout length (10 mm.) and head length (37.3 mm.) this specimen, of 117.5 mm. standard length, falls within the range of *Bramocharax bransfordi dorioni*. In dentition, however, *S. macrocephalus* differs from all species of *Bramocharax* in having no diastemas among the inner premaxillary and mandibular teeth and in having the second and third mandibular teeth of equal size. The holotype was kindly sent for study by Dr. P. Humphry Greenwood.

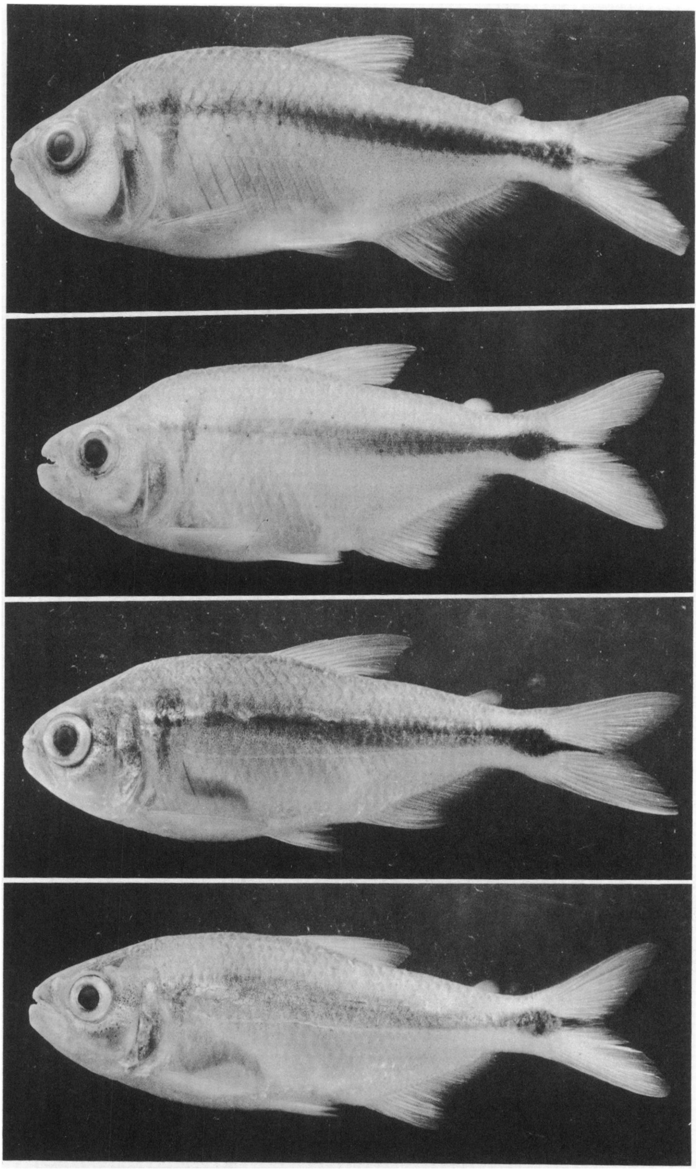

FIG. 11. Variations in body form, eye size, and snout length in *Astyanax fasciatus* from karst region of Alta Verapaz, Guatemala. *Top*: Río Candelaria Yalicar, 81 mm. standard length, AMNH 30162. *Second from top*: Río San Simón, 70 mm. standard length, AMNH 30163. *Bottom two*: Río Senizo, 71 mm. (second from bottom) and 75 mm. standard length (bottom), AMNH 30161.

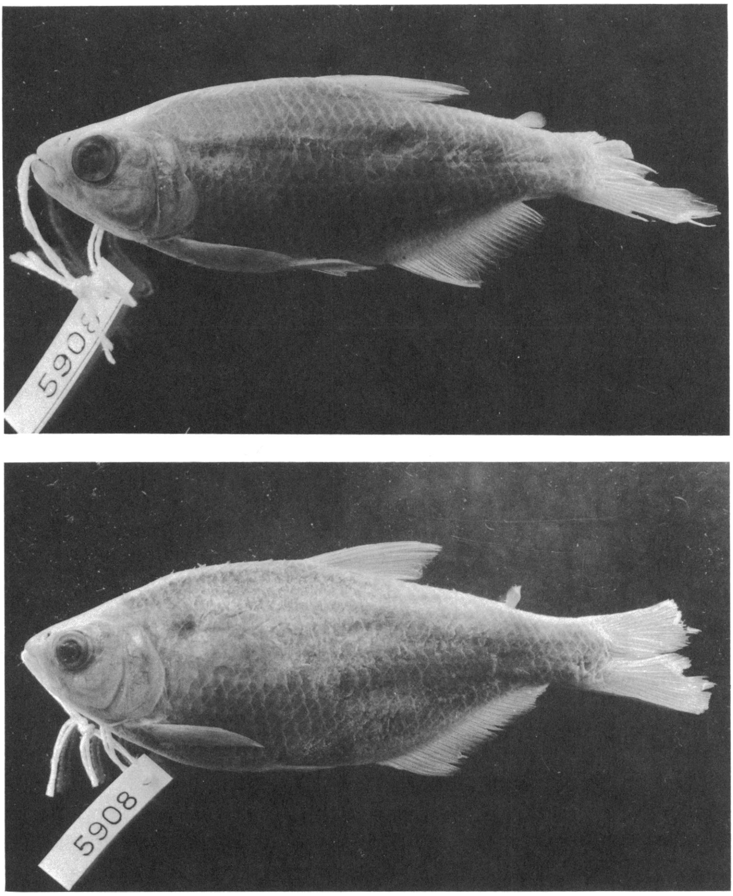

FIG. 12. Paratypes of *Astyanax nasutus* from Lake Nicaragua, Field Museum of Natural History 5908. *Top*: adult male, 66 mm. standard length. *Bottom*: adult female, 82 mm. standard length.

The analysis above, summarized in table 2, indicates that *Bramocharax baileyi* is the most primitive member of its group, sharing few of the specialized features of dentition, and no advanced pigmentary traits with *b. dorioni* or *b. bransfordi*. In the matter of relative snout length it is less specialized than *b. bransfordi* and somewhat more so than *b. dorioni*. *Bramocharax baileyi* is therefore inferred to be the sister group of the more closely related *b. dorioni* and *b. bransfordi*. That phylogenetic inference has three noteworthy zoogeographic implications, namely, that the genus

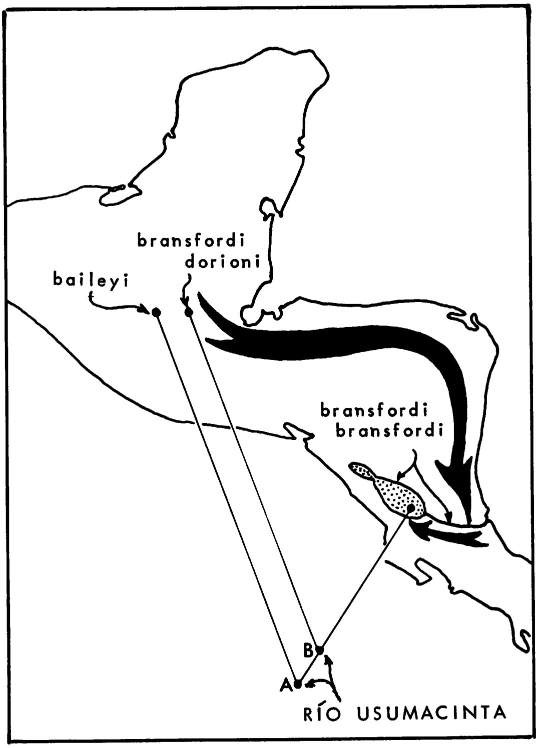

FIG. 13. Zoogeographic hypothesis of origin and dispersal of *Bramocharax* in Central America based on fewest assumptions regarding actual distributional evidence. Hypothetical common ancestor of group (A) is inferred to have been in the Río Usumacinta where *baileyi* (primitive sister group of the other forms) is now. Hypothetical common ancestor of *b. dorioni-b. bransfordi* complex (B) is also inferred to have been in the Río Usumacinta where *b. dorioni* is now confined. Hypothetical ancestor (B) would therefore also have given rise to a population that dispersed southeastward and would most likely have entered the Río San Juan drainage of Nicaragua and Costa Rica via its tributary waters. Once having entered the Río San Juan Basin, and having differentiated as *b. bransfordi*, it would have moved upstream to the great lakes of Nicaragua. This hypothesis implies only a single major dispersal. All other hypotheses would require the dispersal of two or more ancestral taxa and the subsequent disappearance of descendent taxa from their ancestral point of origin.

originated in the Río Usumacinta Basin, that the *dorioni-bransfordi* complex also originated there, and that a member of the *dorioni-bransfordi* complex might be expected to be found somewhere in the largely unexplored waters of eastern Guatemala, Honduras, and Nicaragua between the Río

Usumacinta and the Río San Juan (fig. 13). Bussing (1967) proposed that the presence of *bransfordi* in the lower San Juan and its tributaries may indicate that this form is spreading southward from a population center in the great lakes of Nicaragua. Our present knowledge of the forms of *Bramocharax* and the overall zoogeographic picture hypothesized here is more consistent with an interpretation of the Río San Juan population as stemming from an older invasion of Nicaragua that ultimately found its way upstream to the lake basins. Hence, the populations in Lake Nicaragua and Lake Managua might be of more recent origin than all other populations of *Bramocharax*.

LITERATURE CITED

Bussing, W. A.
1967. (April) New species and new records of Costa Rican freshwater fishes with a tentative list of species. Rev. Biol. Trop., for 1966, vol. 14, no. 2, pp. 205–249.

Eigenmann, C. H.
1917-1927. The American Characidae. Mem. Mus. Comp. Zool., Cambridge, vol. 43, pts. 1–4, pp. 1–428.

Eigenmann, C. H., and G. S. Myers
1929. The American Characidae. Mem. Mus. Comp. Zool., Cambridge, vol. 43, pt. 5, pp. 429–558.

Rosen, D. E.
1970. A new tetragonopterine characid fish from Guatemala. Amer. Mus. Novitates, no. 2435, pp. 1–17.