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A New Tetragonopterine Characid Fish From Guatemala

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The present paper is the third in a series describing an endemic upland fish fauna from an intermontane basin that drains into the Río Usumacinta system from Alta Verapaz, Guatemala. The present report is an account of a hitherto unknown characid of the genus *Bramocharax*. The area of endemism, known as the Chajmaic Valley, was first explored ichthyologically in 1963 and was visited again in 1968 for additional study and collecting. Reeve M. Bailey and I made an air and ground survey of the valley and adjacent areas, which resulted in the discovery that the region of ichthyofaunal endemism extends beyond the limits of the Chajmaic Valley. The two fishes previously described from the Río Chajmaic, the sole drainage system of the valley, were poeciliids: *Scolichthys iota* Rosen (1967) and *Xiphophorus helleri signum* Rosen and Kallman (1969). The genus *Scolichthys* is represented by a second species, *S. greenwayi* Rosen, from a more westerly stream that also drains into the Usumacinta system but that was not previously known to be topographically isolated from the main river basin. During the 1968 air survey, it was seen that at least one of the two streams from which *S. greenwayi* had been taken passes under a low limestone ridge before emerging from the westerly foothills of the Sierra de Chama. Subsequent fishing in the isolated westerly basin, the Río Dolores, resulted in the collection of additional examples of the genus *Bramocharax*. Prior to 1968,

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Bramocharax was known in Guatemala only from unreported specimens from the easterly Chajmaic Valley. The air survey, and recently completed topographic maps of Alta Verapaz (see sheet 2163 III; Guatemala, 1:50,000; Dirección General de Cartografía, 1963), revealed that between the Río Dolores and Río Chajmaic there is a third intermontane basin, the Río Candelaria Yalicar, without any known surface drainage. All three rivers lie along an east-west axis. The Río Chajmaic drains eastward in its valley and flows into the upper Río de la Pasión through a subterranean passage. The Río Dolores flows westward and northward and, through its subterranean channel, joins the Río Icvolay, a tributary to the Río Salinas. The Río Candelaria Yalicar flows in an easterly direction and may have an underground connection with the basin of the Río de la Pasión, but as we have not yet had an opportunity to visit the Candelaria Valley we can say no more about it now.

For more than half a century *Bramocharax* was known only from Nicaragua from Gill's *bransfordi* and Meek's *elongatus.* Additional specimens, identified as *bransfordi,* were collected by Bussing in Costa Rica and recently reported (1967). The Guatemalan form described below is distinctly different from each of the more southern representatives of the genus.

Of the southern populations, Bussing remarked that a faunal assemblage including *Bramocharax* probably had its origin in the great lakes of Nicaragua and ". . . seems to be moving southward along the broad lowlands of Atlantic Costa Rica." The known Nicaraguan and Costa Rican populations are, however, restricted to a single drainage system, the Río San Juan, which includes the great lakes of Nicaragua. With the discovery of the Guatemalan form, all that can be said about *Bramocharax* is that it may at one time have been more widely distributed (fig. 1). On the basis of inferred relationships of several of the montane Usumacinta fishes to groups now distant from Guatemala, Rosen (1967, pp. 14–15) hypothesized that, at least in Guatemala, the upland isolated valleys may constitute a refuge for parts of an older fauna that was once widespread in Central America.

Acknowledgments

It is a pleasure to acknowledge the assistance of colleagues and friends who have joined me in the field work, especially Drs. Klaus D. Kallman and Reeve M. Bailey, and Messrs. Robert C. Dorion, and Roderico Anzueto. Miss Robin Ingle helped prepare the drawings. The work was supported by funds from, and by the encouragement of, Mr. James C. Greenway.

Paratypes of *Bramocharax elongatus* Meek were lent by Loren P. Woods, Field Museum of Natural History, (F.M.N.H.); the syntypes of *Bramocharax bransfordi* Gill, as well as some Lake Managua material were made available by Stanley H. Weitzman, United States National Museum, Smithsonian Institution (U.S.N.M.); Costa Rican material, collected by W. A. Bussing, was lent by the Los Angeles County Museum of Natural History, (L.A.C.M.). Other materials are from the collections of the American Museum of Natural History (A.M.N.H.), and the University of Michigan Museum of Zoology (U.M.M.Z.).

Bramocharax bransfordi dorioni, new subspecies

Figures 1, 2, 4, 6–9; table 1

MATERIAL: The holotype (A.M.N.H. No. 29411) is an adult male, 99.5 mm. in standard length, obtained with rotenone in the Río Semococh, tributary to the Río Chajmaic, a headwater source of the Río de la Pasión (Río Usumacinta Basin) 15 kilometers by road south of Sebol, Alta Varapaz, Guatemala, on March 14, 1963 by K. D. Kallman and D. E. Rosen. Taken with the holotype were 52 juveniles and adults (A.M.N.H. No. 29412) 52 to 167 mm. in standard length. Additional specimens were secured in Alta Verapaz in 1968 by R. M. Bailey, D. E. Rosen and party, as follows: 27 adults (U.M.M.Z. Nos. 187926 and 187926-S; A.M.N.H. No. 27816-DS), 117 to 193 mm. in standard length, taken by gill-net in the Río Chajmaic just upstream of Chajmaic, March 7–8; 22 juveniles and adults (A.M.N.H. Nos. 29413 and 29413-WS), 29 to 94 mm. in standard length, rotenoned in the second arroyo (unnamed) above the mouth of the Río Semococh into the Río Chajmaic, March 8; 11 juveniles and adults (U.M.M.Z. No. 187930), 43 to 110 mm. in standard length, rotenoned in the lower 200 meters above the mouth of the Arroyo Salaguna, the first arroyo below the Río Semococh into the Río Chajmaic, March 8; 6 juveniles (A.M.N.H. No. 29414) 27 to 43 mm. in standard length, rotenoned in a woodland pool 13 kilometers southwest of Sebol in the Chajmaic Valley, March 9; 8 juveniles (U.M.M.Z. No. 187944) 33 to 51 mm. in standard length, rotenoned in the Río Semococh, Río Chajmaic system, where it is crossed by Highway No. 5, 15 kilometers by road south of Sebol (the type locality), March 9; 2 juveniles (A.M.N.H. No. 29415), 24 to 66 mm. in standard length, rotenoned in the Río Dolores, Río Salinas system, along the shore at Yaxcabnal, March 21.

DIAGNOSIS: A form of *Bramocharax* differing from the other nominal species in having the snout nearly equal in length to the diameter of

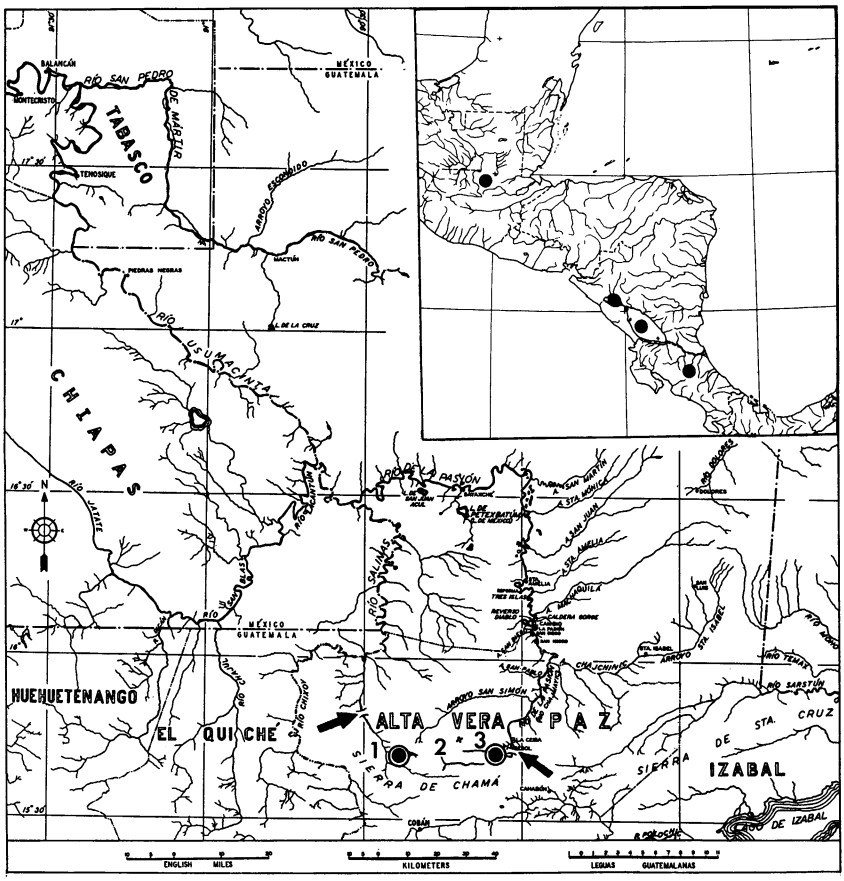

FIG. 1. El Petén, Guatemala and adjacent regions, showing collecting localities in Alta Verapaz for *Bramocharax bransfordi dorioni,* new subspecies, and inset map of Central America showing distribution of known populations of *Bramocharax.* In Guatemala, locality 1 is the Río Dolores, locality 2 the still unexplored Río Candelaria Yalicar, and locality 3 the Río Chajmaic. The arrows point to subterranean river channels. The base map of Guatemala is modified from one compiled by Carl L. Hubbs and Henry van der Schalie in 1937.

the orbit (rather than notably longer); in having the anterior premaxillary canines fitting within sockets in the lower jaw when the mouth is closed (rather than overhanging the lower lip); and in having the posterodistal margin of the maxilla recurved (rather than straight).

DESCRIPTION: Dorsal fin rays, 10 (4), 11 (45); anal fin rays, 25 (1), 26 (4), 27 (16), 28 (23), 29 (4), 30 (1); pelvic fin rays (sum of right and

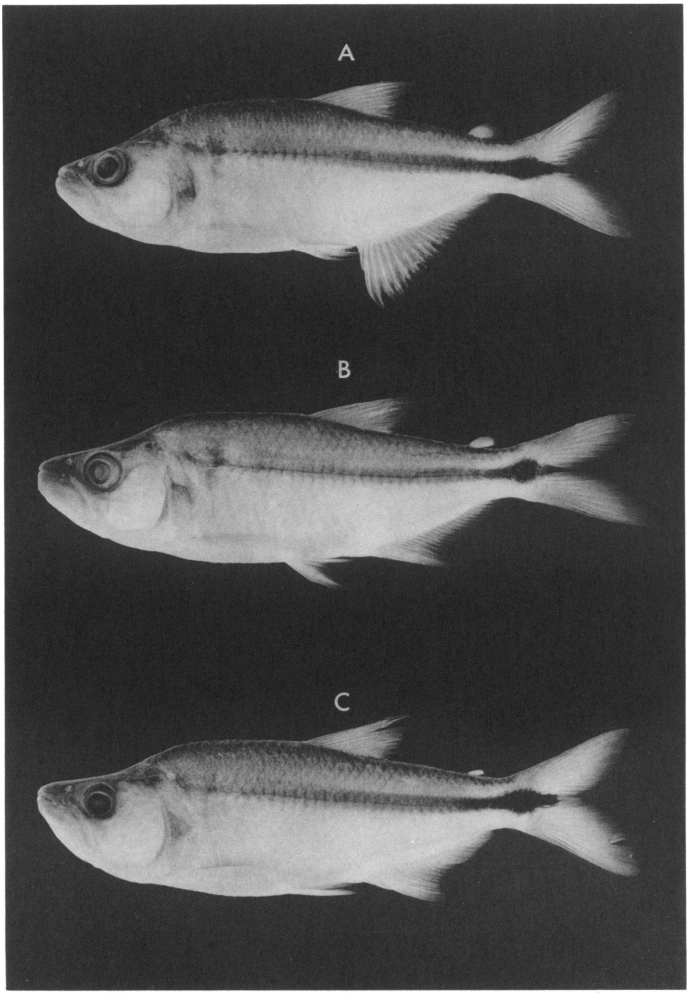

FIG. 2. *Bramocharax bransfordi dorioni,* new subspecies. A. Holotype, an adult male, 99.5 mm. in standard length, A.M.N.H. No. 29411. B., C. Adult females taken with the holotype, A.M.N.H. No. 29412. B. Female, 115.0 mm. in standard length. C. Female, 136.5 mm. in standard length.

left counts), 25 (2), 26 (6), 27 (11), 28 (10), 29 (7), 30 (6), 33 (1); lateral line scales, 37 (8), 38 (18), 39 (16), 40 (6); scale rows on left side (counted obliquely backward from pelvic fin origin), 13 (1), 13½ (15), 14 (11), 14½ (22). Proportional measurements that distinguish *dorioni* are given in figures 8 and 9. The snout length measurement appears to be the most

immediately useful in comparing *dorioni* with other *Bramocharax,* as the snout is equal in length to the diameter of the orbit in *dorioni* and notably longer than the orbit diameter in Nicaraguan forms. A plot of snout length against standard length shows, surprisingly, that relative snout length does not differ in *dorioni* and the specimens from Nicaragua and Costa Rica (fig. 8). Relative head length does, however (fig. 9), and

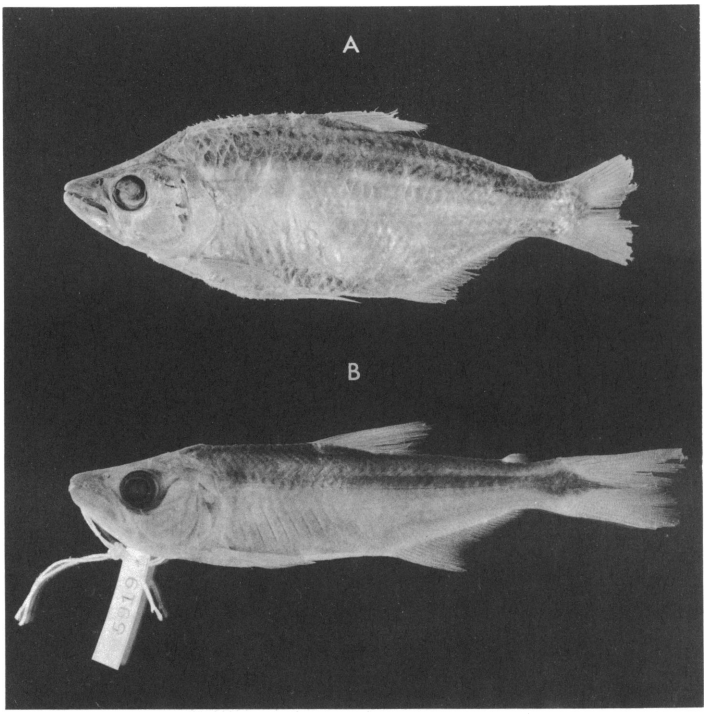

FIG. 3. *Bramocharax bransfordi bransfordi* Gill. A. Syntype of *Bramocharax bransfordi* Gill, U.S.N.M. No. 16885. B. Paratype of *Bramocharax elongatus* Meek, F.M.N.H. No. 5919.

an index derived by dividing head length into snout length plotted against standard length shows that the two populations are well separated from each other in any given size class. The differences between *dorioni* and what has been called *bransfordi* and *elongatus* amounts to the eye being more posteriorly situated in the head in the Nicaraguan and Costa Rican material. Measurements of eye size, and of various other body proportions, failed to separate *dorioni* from the Nicaraguan and Costa

Rican specimens. In life, the body color of *B. bransfordi dorioni* is light amber, the gill cover has silvery reflections, and the fins of large adults, particularly the pelvic, anal, and caudal fins, are rosy. The pectoral and dorsal fins are clear or pale yellow. In half-grown and juvenile *dorioni* the fins usually are clear or pale yellow; the caudal fin sometimes has a pinkish wash.

Minute tubercles are present on the pelvic and anal fin rays of adult males (fig. 7).

ETYMOLOGY: The trivial name *dorioni* was selected as an expression of gratitude to Mr. Robert C. Dorion who has provided continuing assistance for our field efforts in Guatemala since 1963, and whose companionship and hard work during several field trips have always been greatly appreciated.

TAXONOMY AND COMPARISONS: Until 1967, the genus *Bramocharax* Gill and Bransford (1877) was understood to include two nominal species, *B. bransfordi* Gill, in Gill and Bransford (1877), from Lake Nicaragua, and *B. elongatus* Meek (1907) from Lake Managua, Nicaragua. *Bramocharax elongatus* was separated from *bransfordi* by Meek entirely on the basis of its lesser body depth (see fig. 3). When Bussing (1967) reported on collections of *Bramocharax* from Costa Rica (identified by Bussing as *bransfordi*), he commented that the body depth in two large Costa Rican specimens (103 mm. and 123 mm. in standard length) is intermediate between depth values given by Meek for the two nominal species. He predicted that further collecting and comparison would disclose that there is only one valid species of *Bramocharax*. Two of Bussing's specimens (from the Río Chiripiqui, a tributary of the Río Sarapiqui, Río San Juan drainage) were available for study, one of which is exceedingly small (22.6 mm. in standard length). In the larger specimen (102.5 mm. in standard length), the snout is definitely longer than the diameter of the eye (fig. 5A), although it is relatively shorter than the snout of specimens from Nicaragua. The front upper canines in the larger specimen from Costa Rica either have been shed or broken off, but from the position of the tooth sockets, one may deduce that it is possible these teeth, when present, overhung the lower lip. The snout-head length indices of Bussing's specimens are distinctly different from the indices of *dorioni* and like those of Nicaraguan *bransfordi* (fig. 9), however.

Four additional specimens from Costa Rica, taken by Royal D. Suttkus and party (Tulane University Collections No. 25081, Río Sapoá, and No. 24912, Río Sarapiqui, both Río San Juan drainage), also have a *bransfordi* type of snout-head length index (index values of 290–307 in individuals of 49 to 57 mm. standard length) and show the overhanging front canines,

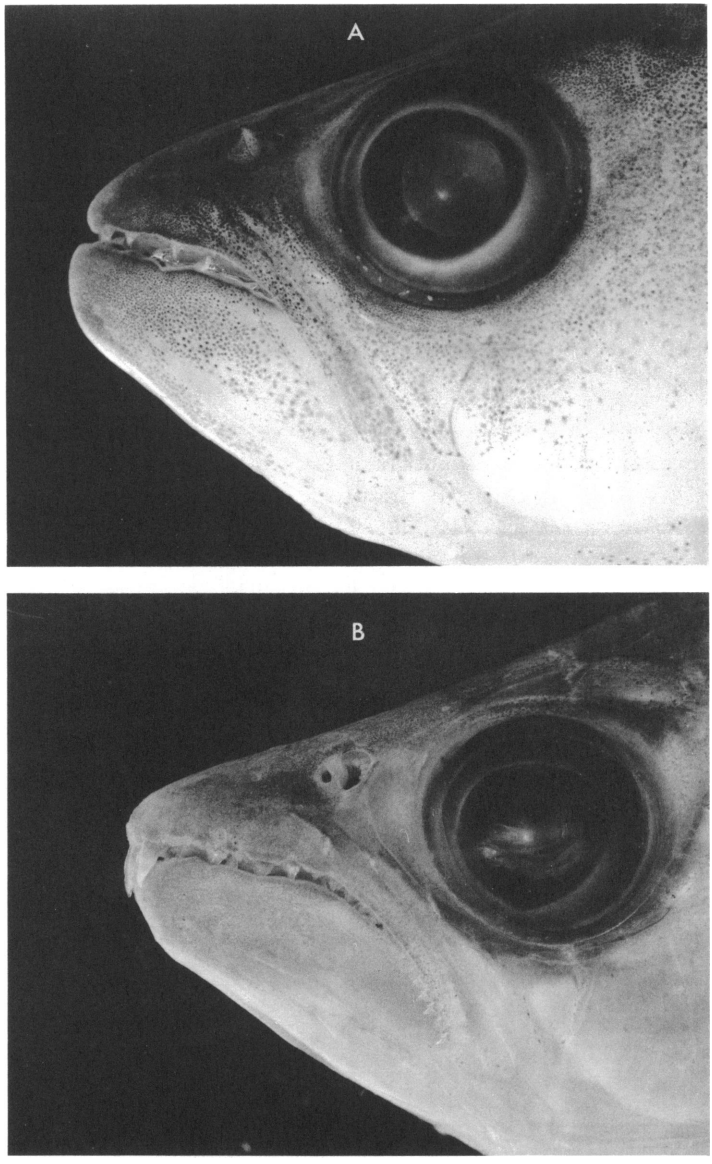

FIG. 4. Anterior head region in *Bramocharax*. A. *Bramocharax bransfordi dorioni,* holotype. B. *Bramocharax bransfordi bransfordi,* F.M.N.H. No. 5919, from Lake Managua. In B, note anterior premaxillary canines overhanging lower jaw.

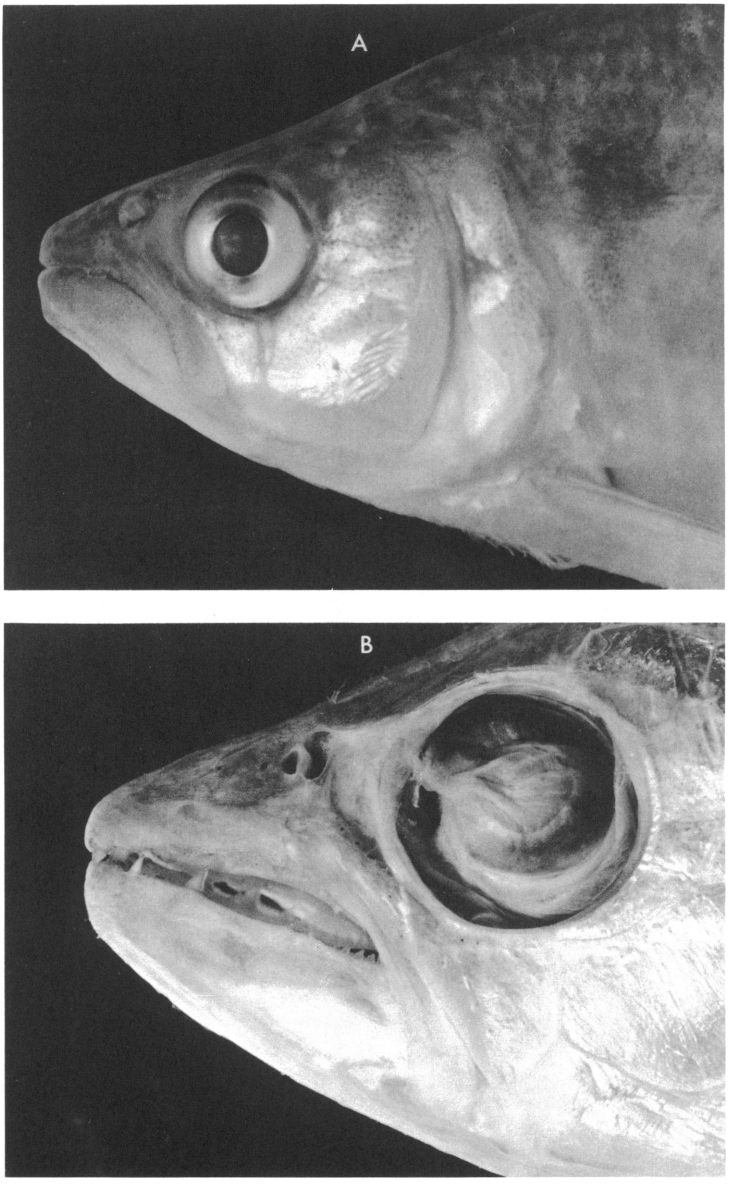

FIG. 5. Anterior head region in *Bramocharax bransfordi bransfordi.* A. Specimen from Río Chiripiqui, Costa Rica, L.A.C.M. No. 9112-4. B. Syntype of *Bramocharax bransfordi,* U.S.N.M. No. 16885, from Lake Nicaragua. Anterior canines are missing in A and broken at the tip in B.

TABLE 1

FIN RAY AND SCALE NUMBER IN THE FORMS OF *Bramocharax*

	B. bransfordi dorioni			*B. bransfordi bransfordi*											
	A.M.N.H. No. 29412			U.S.N.M. No. 16885, Syntypes of *bransfordi*			A.M.N.H. No. 17327			F.M.N.H. No. 5919, Paratypes of *elongatus;* U.S.N.M. No. 78099			L.A.C.M. Nos. 9102-10, 9112-4		
	Río Chajmaic			Lake Nicaragua			Arroyo Tulé into Lake Nicaragua			Lake Managua			Río Sarapiqui System Río San Juan drainage Costa Rica		
	Range	No.	Mean± St. E.	Range	No.	Mean± St. E.	Range	No.	Mean± St. E.	Range	No.	Mean± St. E.	Range	No.	Mean± St. E.
Fin rays															
Dorsal	10–11	(49)	10.9±0.0	11	(3)	11.0 —	10–11	(10)	10.8±0.2	11	(7)	11.0 —	10	(2)	10.0 —
Anal	25–30	(49)	27.6±0.1	28–29	(3)	28.7±0.5	28–31	(10)	29.3±0.3	28–31	(7)	29.7±0.5	31	(2)	31.0 —
Pelvic (Right +Left)[a]	13–16	(49)	15.6±0.1	16–18	(3)	16.7±0.9	16	(10)	16.0 —	16–18	(7)	16.2±0.3	16	(1)	16.0 —
Pectoral (Right +Left)	25–33	(43)	27.9±0.2	30–32	(3)	31.3±0.9	28–34	(10)	29.8±0.3	28–32	(7)	29.6±0.5	30	(1)	30.0 —
Lateral line scales	37–40	(49)	38.4±0.3	37–38	(2)	37.5[b] —	37–39	(10)	38.0±0.2	39–41	(7)	39.7±0.3	37	(1)	37.0 —
Scale rows	13–14½	(49)	14.0±0.2	14½–15	(2)	14.7[b] —	13½–14½	(10)	14.1±1.2	13½–14½	(7)	14.0±1.7	14½	(1)	14.5 —

[a] Counts do not include the pelvic splint.

[b] Counts made from scale pockets only.

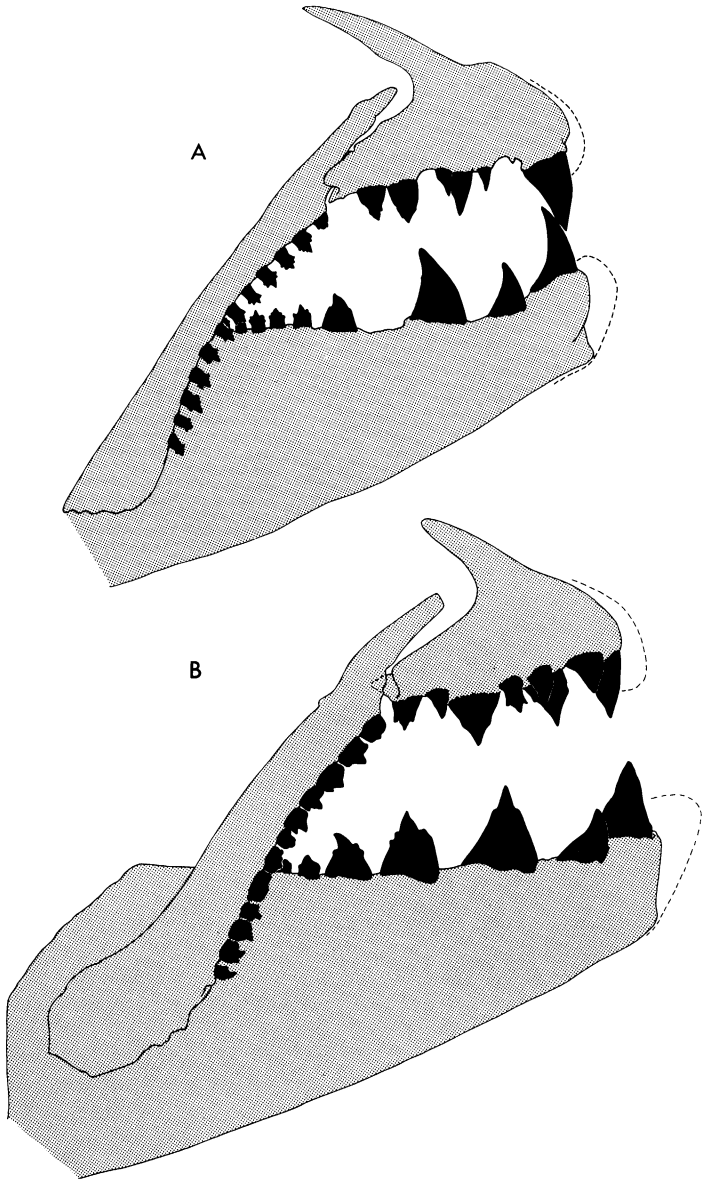

FIG. 6. Upper and lower jaws in *Bramocharax*. A. *Bramocharax bransfordi bransfordi*, F.M.N.H. No. 5919. B. *Bramocharax bransfordi dorioni*, A.M.N.H. No. 29412.

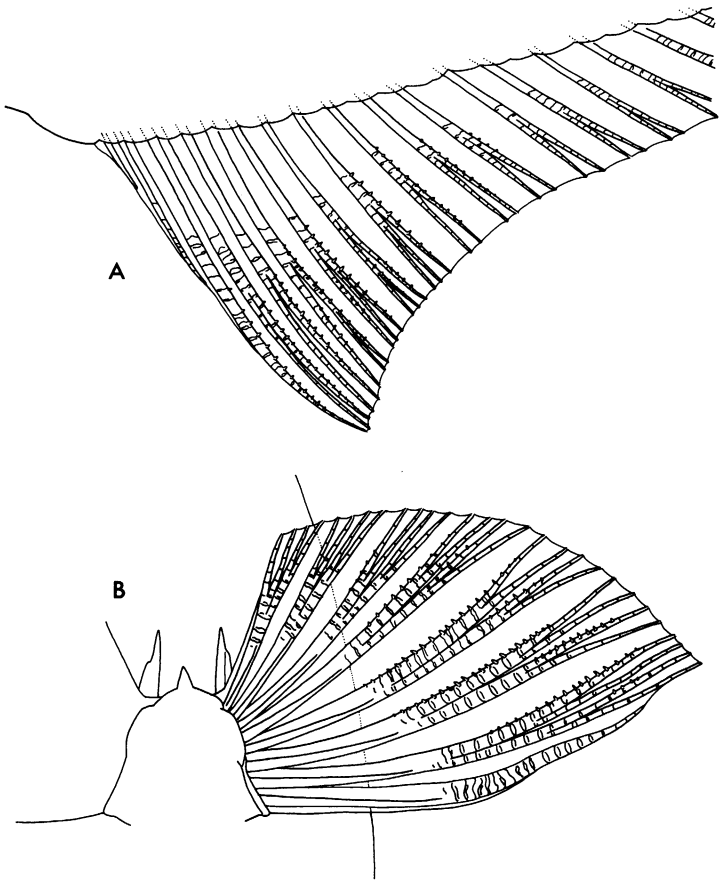

FIG. 7. Fins of adult male *Bramocharax bransfordi dorioni,* showing distribution of tubercles. A. Anal fin. B. Left pelvic fin, ventral view.

as well, making it probable, therefore, as Bussing has said, that all Costa Rican specimens are assignable to *bransfordi.*

The three syntypes of *bransfordi* and a small series of paratypes of *elongatus* were examined (table 1), but no definite inference could be drawn from them regarding the validity of *elongatus* as a distinct species. It was noted, however, that in the smallest of Gill's three specimens (79 mm. in standard length), the length-depth ratio is indistinguishable from that given for *elongatus* (3.8 in standard length as compared with 3.4 to 3.9 given by Meek for *elongatus*). In another series of specimens from Arroyo Tule at San Miguelito on the southeast shore of Lake Nicaragua

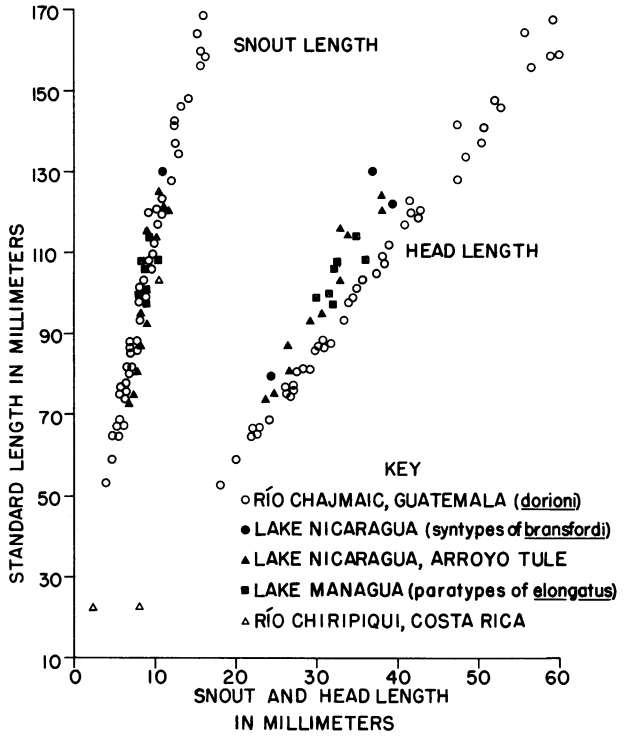

FIG. 8. Snout and head length in the populations of *Bramocharax*.

(A.M.N.H. No. 17327), measurements of body depth would place some individuals in *bransfordi* and others in *elongatus*. The more slender, or *elongatus*-types (with values of 3.4 and 3.5), are males, as indicated by the presence of pelvic and anal fin tubercles; the deeper-bodied *bransfordi*-types are females and juveniles (with values of 2.7 to 3.3). In snout and tooth structure and in snout length (figs. 4–6) *bransfordi* and *elongatus* cannot be separated, and both nominal forms differ from *bransfordi dorioni* in the contrasting characters given in the above diagnosis. It is therefore concluded that there is no evidence for regarding *elongatus* as a valid taxon.

Neither is there evidence for regarding *dorioni* as a full species. Although *dorioni* and *bransfordi* are easily differentiated, the same may be said of many distinct groups recognized as subspecies. The important feature of our knowledge of the forms of *Bramocharax* is that all known populations are allopatric, all are recognizably related, and there are only two morphotypes on which to base a taxonomic decision. Cer-

tainly, no biological criteria can be applied to suggest that any of the populations have reached a specific level of differentiation. It is true that dentitional differences of the sort described here—and even lesser ones—have been used in the past to rank allopatric populations of characids as species. In many cases a statement has accompanied the ranking procedure which calls attention to a tradition or practice for using such criteria. The practice has frequently been arbitrary, and must be so in every case where all known populations of a close-knit group are allopatric and where no experimental work has been done to establish a background of biological data, that would suggest behavioral or genetic isolation. Unfortunately, neither traditions nor well-founded practices relevant to other tetragonopterine genera can be shown to apply decisively to the two forms of *Bramocharax*. To recognize a new species, and to give it appropriate taxonomic status is a major step in systematics and must be based upon something more than the human ability to distinguish an animal from its nearest relative.

In Gill and Bransford's (1877) original diagnosis of *Bramocharax,* the premaxillary teeth are described as uniserial. In *bransfordi,* and in *dorioni,* there are two distinct kinds of teeth distributed along a rather narrow dental margin: small, usually cuspidate teeth, and much larger compressed conical teeth. The two kinds of teeth tend to overlap on the premaxillary, and where they do, the smaller teeth are always external to the larger ones. It is thus more accurate to say that the premaxillary teeth are in two series as in related tetragonopterine characids such as *Astyanax*. The jaw teeth in the known forms of *Bramocharax* may be redescribed as follows: Premaxillary teeth in two closely approximated series, consisting of 3 or 4 enlarged teeth on the inner series (unicuspid in large adults, with one or more lateral cusps in small adults and juveniles), and 2 to 6 small, usually cuspidate, teeth on the outer series. Maxillary teeth small, cuspidate (rarely unicuspid), 6 to 19 in number. Dentary teeth in a single series, the 3 or 4 anterior ones much enlarged and conical, occasionally with small lateral cusps, and separated by large diastemas; the 6 to 8 posterior teeth abruptly smaller, close-set, and cuspidate. In specimens of *dorioni* it was noted that in the premaxillary, replacement teeth for the outer row develop in lacunae within the bone, whereas replacement teeth for the enlarged, inner ones develop in soft tissue along the upper, oral margin of the bone. This difference in the site of replacement teeth supports the idea that the premaxillary teeth belong to two distinct series.

Eigenmann and Ogle's (1907, p. 32) figure of one of the larger of the three syntypes of *bransfordi* and of the snout of—presumably—another, is

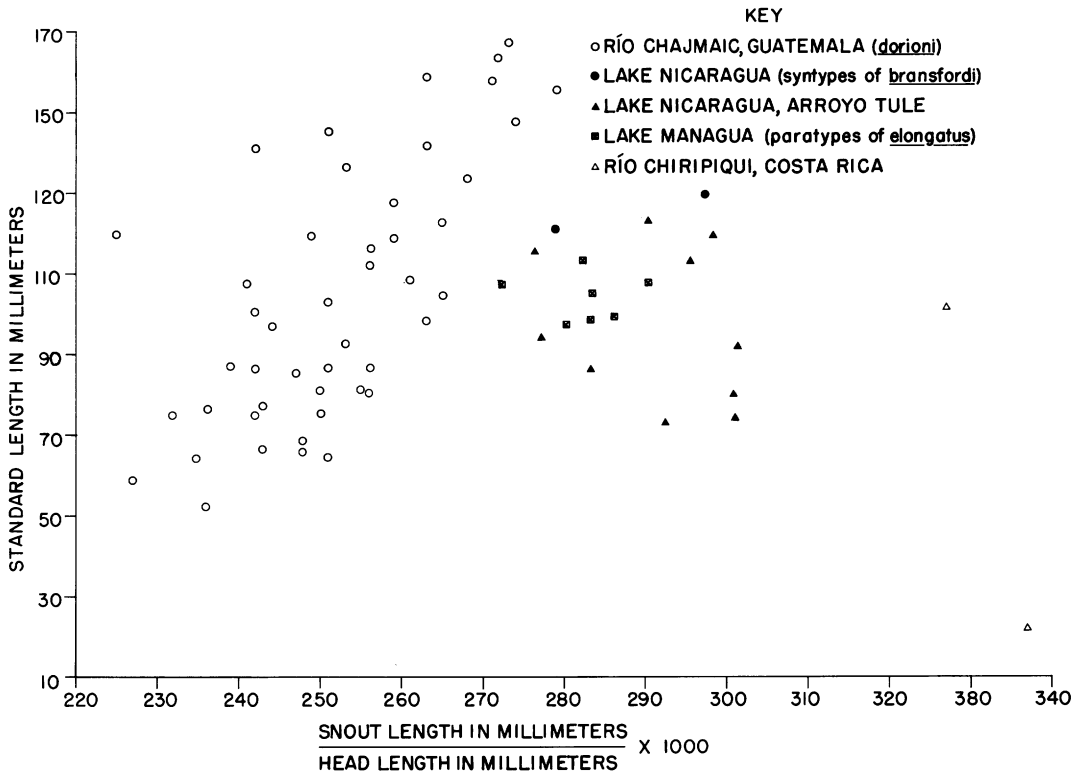

FIG. 9. Snout-length/head-length indices in the populations of *Bramocharax*.

somewhat misleading, for the drawings give the impression that the lower jaw is a bit longer than the upper. That the jaws in *bransfordi* are at least subequal, or that the upper jaw is very slightly longer than the lower, is shown in figures 4 and 5. Were this not the case, the anterior premaxillary canines would not be in position to lie over the lower lip when the mouth is closed. The position of these teeth, whether overhanging the lower jaw or fitting in sockets between the enlarged anterior teeth of the dentary, partly as a function of relative snout length, is one of the major differences between the Guatemalan and the Nicaraguan and Costa Rican forms of *Bramocharax.*

Other differences not yet noted between the Guatemalan and Nicaraguan forms involve fin ray and scale number.

Meek's specimens from Lake Managua have slightly higher lateral line scale counts than all other specimens of *Bramocharax.* The estimated number of lateral line scales in the types of *bransfordi* is lower than in *dorioni,* and the estimated number of scale rows is higher. Scale number in the types of *bransfordi* was estimated from the number of now empty scale pockets, and the scale pockets themselves are badly damaged. In consequence, no significance is attached to the estimated differences in scale number between *dorioni* and Gill's Lake Nicaragua specimens. All samples of *bransfordi bransfordi* examined have a slightly higher average anal and pectoral fin ray number than *bransfordi dorioni* (table 1).

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