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Karyology of the Cyprinodontoid Fishes of the Mexican Family Goodeidae

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Karyotypes from 60 populations classified in 17 genera and 35 species of Mexican fishes of the autochthonous family Goodeidae vary from 24 metacentric to 48 subtelocentric-telocentric chromosomes in the diploid complement. About two-thirds of the family have 2n = 48 with terminal or near-terminal centromere positions, a condition regarded as ancestral for goodeids. Reduction of chromosome number has occurred solely by the formation of metacentric elements by Robertsonian fusion of pairs of (probably subtelocentric or acrocentric) chromosomes. It is not possible to determine relationships of the Goodeidae totally on the basis of karyotypes.

THE Goodeidae, a small, diversified family of viviparous cyprinodontoid fishes, is confined to and evidently originated on the Mesa Central of México (Fig. 1) where its center of abundance lies in the well-isolated Río Lerma basin. (This is not the appropriate place to discuss the recent proposal [Parenti, 1981] to include the Nevadan cyprinodontoid genera *Empetrichthys* and *Crenichthys* in the Goodeidae. Those two genera have been karyotyped [Uyeno and Miller, 1971, and subsequent unpublished information]. A detailed report on the karyotypes of these two genera is planned.) Here an adaptive radiation of significant proportions has taken place during the evolution of approximately 36 species since Miocene time, or probably before, since the late Miocene fossil genus *Tapatia* had already developed a highly-derived anal fin (Smith and Miller, 1981).

The last revision of the Goodeidae (Hubbs and Turner, 1939) delineated species and assessed relationships primarily from ovarian characteristics and trophotaeniae. The latter, anal ribbon-like or rosette structures known in the embryos of all but one species (*Ataeniobius toweri*), presumably function in the uptake of

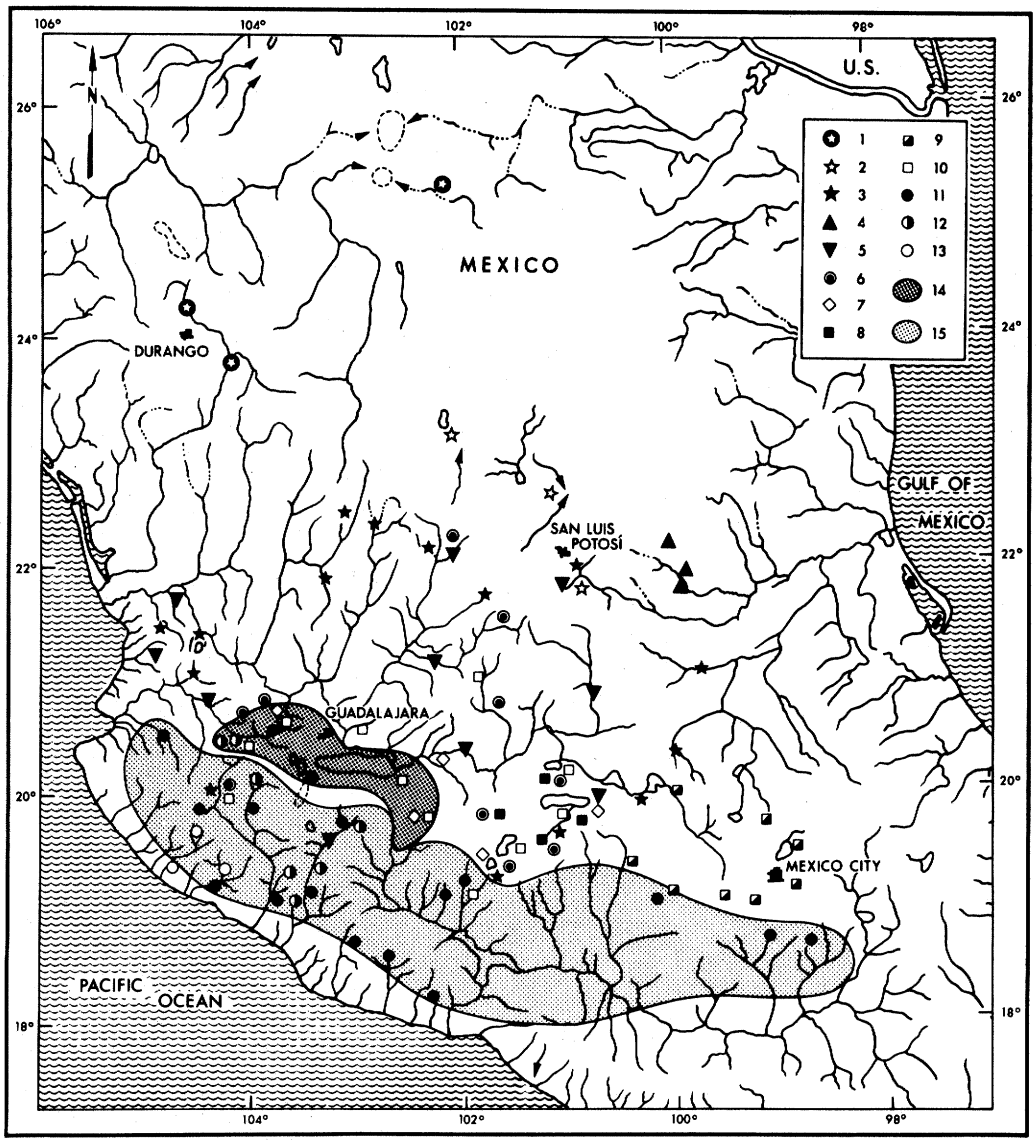

Fig. 1. Distribution of the genera of the Goodeidae. Only localities near outer limits of distribution are plotted for each genus. 1 = *Characodon*, 2 = *Xenoophorus*, 3 = *Goodea*, 4 = *Ataeniobius*, 5 = *Xenotoca*, 6 = *Allotoca*, 7 = *Skiffia*, 8 = *Hubbsina*, 9 = *Girardinichthys*, 10 = *Zoogoneticus* and *Neoophorus*, 11 = *Ilyodon*, 12 = *Allodontichthys*, 13 = *Xenotaenia*, 14 = area of greatest concentration (11/17) of genera, 15 = area of concentration of *Ilyodon*. Genera in 14 are: *Allodontichthys*, *Alloophorus*, *Allotoca*, *Ameca*, *Chapalichthys*, *Goodea*, *Ilyodon*, *Neoophorus*, *Skiffia*, *Xenotoca* and *Zoogoneticus*.

nutrients released into the ovary, since the cells of the trophotaenial epithelium are structurally indistinguishable from those of the intestinal epithelium of the embryo (Wourms and Cohen, 1975). The number, length and histological type of trophotaeniae and, in the ovary, the location of ovigerous tissue and nature of the septum, formed the basis for dividing the family into 11 phyletic lines comprising four subfamilies, 18 genera and 24 species. Seventeen living genera and 33 described species are currently recognized (Miller and Fitzsimons, 1971; Fitzsimons,

1972, 1979, 1981; Kingston, 1978; Miller and Uyeno, 1980; Smith and Miller, 1980).

The first published karyotype for the Goodeidae, that of *Ameca splendens*, was prepared by Uyeno and given by Miller and Fitzsimons (1971), who presented a list of diploid chromosome numbers for 34 other goodeids. Those numbers, augmented by data from additional species reported herein, show that karyotypes are rather diverse in goodeids (2n = 24 to 48) when compared to some other groups of similar size (e.g., the Centrarchidae—Busack and Thorgaard, 1980; and *Cyprinodon*—Stevenson, 1981). Karyotypes have proven helpful in the interpretation of taxonomic categories and in the study of hybrid intermediacy, wherein goodeid species with distinctive chromosome number and/or morphology, when crossed, produced a precisely intermediate F_1 karyotype (Fitzsimons, 1974). Subsequently, nine additional goodeid karyotypes have been presented in papers by Benirschke and Hsu (1971, prepared by Uyeno), Fitzsimons (1972, 1974), Uyeno and Miller (1972) and Smith and Miller (1980).

Here we summarize what is known about karyotype variation in goodeids and discuss the limitations and significance of karyotype studies for fish systematics (Uyeno and Miller, 1973). Further consideration of goodeid interrelationships awaits examination of additional karyotypes, more extensive meristic and morphometric data, biochemical comparisons (currently being pursued by Bruce J. Turner of Virginia Polytechnic Institute and State University, Blacksburg), osteological studies and additional morphological and behavioral observations—especially on the challenging genus *Ilyodon*.

Materials and Methods

Goodeids for karyology were collected from the following states of México. **Durango:** Los Berros, 4 km NE El Salto, ca 40 km SE Durango, M68-41 (*Characodon lateralis*). **Nayarit:** Manantial El Sacristán, 1.3 km NW Tepic plaza, M55-72 (*Xenotoca eiseni*); Río San Leonel, ca 25 km SE Tepic, M70-31 (*Xenotoca eiseni*). **Aguascalientes:** Presa El Jigante, near Santa María de Gallardo, 20.8 km NE Hwy. 45 on road to Loreto (at La Dichosa), M68-29 (*Allotoca dugesi, Xenotoca variata*). **San Luis Potosi:** Ojo de Agua de Moctezuma, ca 1.6 km SW of town, ca 48 km N Ahualulco, M70-6 (*Xenoophorus captivus*); Presa de San Ysidro, ca 3 km SW Jesús María, M70-7 (*Xenoophorus captivus*); Río Santa María, ca 1.6 km S Villa de Reyes, M68-21 (*Goodea gracilis, Xenotoca variata*); Río Santa María, ca 5 road km above Santa María del Río, M66-8 (*Xenoophorus captivus*); Río Villeto, trib. Río Santa María, 10.1 km S Hwy. 57 crossing of Río Santa María, below bridge, M76-10 (*Xenoophorus captivus*); La Media Luna, at western outlet ditch by road, 12.2 km SSW Ríoverde, M68-18 (*Ataeniobius toweri*). **Guanajuato:** Ojo de Agua de Santiaguillo, 1.6 km NE and 2.4 km N San Francisco del Rincón, M70-9 (*Zoogoneticus quitzeoensis*); Río Turbio, 10 km E Penjamo at Hwy. 110 bridge, M76-22 (*Alloophorus robustus, Goodea atripinnis*); Lago Yuriria, M70-28 (*Allotoca dugesi*). **Querétaro:** Río San Juan del Río, just below old bridge, San Juan del Río, M76-25 (*Goodea gracilis*). **Jalisco:** Río Potrero Grande, 8.8 km W. Ameca, M71-5 (*Neoophorus* sp.); Presa de la Vega, in Río Ameca, 32 km W jct. Hwy. 15 and Hwy. 70 (to Ameca), M66-16 (*Goodea atripinnis, Xenotoca melanosoma*); Río de la Pola, trib. Río Atenguillo, 40 km W Ameca, M70-10 (*Allodontichthys* sp., *Ilyodon* sp.); Río Teuchitlán below Teuchitlán, M66-17 (*Ameca splendens*); same locality, M70-11 (*Skiffia francesae*); same locality, H76-15 (*Xenotoca melanosoma*); marshy roadside on S side of road across Laguna Magdalena, M70-12 (*Allotoca maculata*); trib. Río Purificación crossed by Hwy. 80, 0.8 km W of turnoff to Purificación, M66-15 (*Xenotaenia resolanae*); outlet of Presa Santa Rosa, 3.7 km E of turnoff Hwy. 80, 4.8 km S Unión de Tula, M76-35 (*Ilyodon furcidens*); Río Tamazula at Hwy. 110 bridge, 4.8 km S Ciudad Guzmán turnoff, M66-13 (*Xenotoca eiseni, X. melanosoma*); same locality M68-30 (*Allodontichthys tamazulae, Ilyodon furcidens*); Río Tuxpan, ca 1 km above Atenquique in small trib. from E and main river, M70-13 (*Xenotoca melanosoma*); trib. Río Tuxpan, just above Atenquique, M71-7 (*Ilyodon furcidens*); Río Terrero, 0.8 km W 21 de Noviembre, 15.7 km N Pihuamo (Hwy. 110), M71-8 (*Ilyodon furcidens, I. xantusi, Allodontichthys hubbsi*); same locality, M76-30 (*Allodontichthys tamazulae*). **Colima:** Río de Comala, just above and below 2nd bridge S. Comala, M70-14 (*Allodontichthys zonistius, Ilyodon furcidens, I. xantusi*). **Michoacán:** Río Tanhuato NE edge Tanhuato, M70-16 (*Chapalichthys encaustus*); El Agua de Zapote de Tocumbo, Tocumbo, M71-9 (*Chapalichthys pardalis*); Lago Camécuaro, SE Zamora, M76-26 (*Skiffia multipunctata*); Río Santa Catarina, just above Presa Santa Catarina, E Uruapan, M70-22, (*Neoophorus catarinae*); Río Cupatitzio, just below Presa Cupatitzio, M70-23 (*Alloophorus robustus, Ilyodon whitei*); SE end Lago Zirahuén, M70-24 (*Allotoca dugesi*); same locality, M76-18 (*Alloophorus robustus, Neoophorus meeki*); spring at Rancho El Molino, ca 11 km NE of Pátzcuaro, M70-25 (*Goodea luitpoldi, Neoophorus diazi*); same locality, M76-17 (*Skiffia lermae*); Canal de Queréndaro at Tzintzimeo, 8.8 km E Alvaro Obregón, M70-26 (*Alloophorus robustus*); same locality, M71-11 (*Hubbsina turneri*); same locality, M76-15 (*Goodea atripinnis, Skiffia bilineata*); S end Lago de Cuitzeo, M70-27 (*Xenotoca variata*). **México:** Río Lerma, just below base of Presa Alzate, M70-19 (*Girardinichthys multiradiatus*); N side Laguna de Zumpango, M70-30 (*Girardinichthys viviparus*). **Morelos:** Laguna Zempoala, M70-18 (*Girardinichthys multiradiatus*). **Puebla:** Río Nexapa at Puente Tepexcala, ca 32 km WSW Matamoras, M66-12 (*Ilyodon whitei*).

Chromosome microslides were prepared using methods described by McPhail and Jones (1966), Beamish (1970), Beamish et al. (1971) and LeGrande and Fitzsimons (1976). Diploid chromosome numbers were determined by scoring spreads until clear modes were established. Our classification of chromosomes is based on centromere positions, as outlined by Levan et al. (1964). The following abbreviations are employed: M = large metacentric (a result of Robertsonian fusion); m = small metacentric (centromere at median position); sm = submetacentric (centromere at submedian position); smst = submetacentric-subtelocentric (continuous series); st = subtelocentric (centromere at subterminal region); stt = subtelocentric-acrocentric (continuous series); t = acrocentric (centromere at terminal region). Since the karyotypes of many species show chromosomes in a continuous series from acrocentrics (t) to subtelocentrics (st), we have frequently combined them into an acrocentric-subtelocentrics group (stt), as in Table 1. Karyotyped fishes

TABLE 1. KARYOTYPES OF THE GOODEIDAE. M = large metacentric; m = small metacentric; sm = submetacentric; smst = submetacentric-subtelocentric; st = subtelocentric; stt = subtelocentric-telocentric; t = acrocentric. The asterisk indicates that *Skiffia multipunctata* is polymorphic.

Taxon	2n	M	m	sm	smst	st	stt	t
Goodea atripinnis	48			2			46	
Goodea luitpoldi	48			2			46	
Goodea gracilis	48			2			46	
Ataeniobius toweri	48			2			46	
Chapalichthys encaustus	36	12		4		16		4
Chapalichthys pardalis	36	12		2		8		14
Xenotoca variata	48					4		44
Xenotoca eiseni	48					6		42
Xenotoca melanosoma	48					8		40
Alloophorus robustus	30	18	2			2	8	
Ameca splendens	26	22		2				2
Zoogoneticus quitzeoensis	28	20	2				6	
Allotoca maculata	48					4		44
Allotoca dugesi	26	22			2	2		
Neoophorus diazi	46	2				4		40
Neoophorus catarinae	46	2				4		40
Neoophorus sp.	48					6		42
Neoophorus meeki	46	2				6		38
Xenoophorus captivus	48			2		4	42	
Characodon lateralis	24	24						
Allodontichthys tamazulae	48		2	2			44	
Allodontichthys zonistius	48		2	2			44	
Allodontichthys sp.	48		2	2			44	
Allodontichthys hubbsi ♀	42	6	2		2		32	
♂	41	7	2		2		30	
Xenotaenia resolanae	48						48	
Ilyodon furcidens	48					8		40
Ilyodon whitei	48					8		40
Ilyodon xantusi	48					8		40
Skiffia francesae	48		2	6				40
Skiffia multipunctata	46*	2*	2			4		38*
Skiffia lermae	26	22						4
Skiffia bilineata	48		4	2		34		8
Girardinichthys multiradiatus	48					10		38
Girardinichthys viviparus	48					10		38
Hubbsina turneri	48						48	

are preserved in The University of Michigan Museum of Zoology.

RESULTS

Chromosomes from 60 different populations of 35 species in 17 currently-recognized genera were examined and compared. Twenty-two of the 35 species, about two-thirds of the family, have a diploid number of 48 chromosomes. Species with fewer than 48 chromosomes always have large metacentrics, each derived by Robertsonian fusion of two chromosomes. Thus, as in the Cyprinodontidae (Uyeno and Miller, 1971), the number of large metacentrics can be enumerated by subtracting the total chromosome number from 48—e.g., *Chapalitchthys encaustus*, 2n = 36, has 12 large metacentrics (Fig. 2H).

The results of our observations on goodeid karyotypes are summarized in Table 1. They are treated below by genus, in alphabetical order.

Material karyotyped for each species was limited by transport difficulties from the field and by the number of specimens that yielded good

chromosome spreads. At the end of each account the number of specimens examined is given and, separated by an oblique line, the number of spreads with the modal count versus the number of spreads counted; following this is the UMMZ catalogue number. Sexual dimorphism was found only in *Allodontichthys hubbsi*; when more than two specimens are indicated, both sexes are included.

Allodontichthys Hubbs and Turner. 2m 2sm 44stt. Fig. 2A, B. 6M, 4sm, 4stt, 28t in ♀, 7M 4sm 4stt 26t in ♂, of *A. hubbsi* (Uyeno and Miller, 1972).

This genus comprises four known species: *A. tamazulae* Turner and *A. hubbsi* Miller and Uyeno (1980) from the Río Coahuayana basin, *A. zonistius* (Hubbs) from the Río Armería basin, and an undescribed species from the Río Ameca basin—in the states of Jalisco and Colima. Their distribution lies south of the Mesa Central (the southern boundary of which is marked by the east-west Neovolcanic Axis—Maldonaldo-Koerdell, 1964), except for the species in the Río Ameca basin (west of Guadalajara). Two of the southern species (*A. tamazulae* and *A. zonistius*) presumably originated from the Río Ameca representative or its ancestor; *A. hubbsi* was derived from *A. tamazulae* (see below). A similar evolutionary derivation from the highland form is also noted for the genus *Ilyodon*, the poeciliid *Poeciliopsis infans*, the cyprinid *Algansea aphanea* (Barbour and Miller, 1978), and one species of the catostomid genus *Moxostoma* (M. L. Smith, pers. comm.). The geological history of the region is consistent with the origin of these more southerly representatives by stream captures between the Río Armería and Río Ameca basins in Pliocene or Pleistocene time.

The karyotypes of *Allodontichthys* are among the most derived in the family. The three species that are not sexually dimorphic have 2 small metacentrics and 2 submetacentrics, and karyotypes of four populations (two of *A. tamazulae*) are all similar, indicating no major chromosomal rearrangements since the Plio-Pleistocene stream captures and subsequent changes of the drainage patterns which caused their range expansions and the geographical isolation of their populations. These three species are allopatric, so far as known. The fourth species, *A. hubbsi*, is unique for the family in having multiple sex chromosomes, with 2n = 42 and 6 large metacentrics in the female, and 2n = 41 with 7 large metacentrics in the male. This species closely resembles the sympatric *A. tamazulae* and was probably derived from that species or its ancestor (Miller and Uyeno, 1980). Zoogeographic and morphologic information, including karyology, supports a close relationship between these two bottom-dwelling species. (*A. hubbsi* 4 ♀, 60/60; 5 ♂, 60/60, 191682; *A. tamazulae* 3, 48/58, 190892, 209827; *A. zonistius* 1, 3/4, 189593; *A.* sp. 1 ♀, 18/23, 189587)

Alloophorus Hubbs and Turner. 18M 2m 10stt. Fig. 2C.

Alloophorus is monotypic, represented only by *A. robustus* (Bean) which occurs in the lower Río Lerma basin. Karyotypes from four populations are similar. *Alloophorus* is morphologically and zoogeographically closer to *Chapalichthys*, and the karyotype suggests that *Alloophorus* was derived from *Chapalichthys* through fusions of subtelocentric-telocentric elements to form 18 large metacentrics and through changes in centromere position in 2 submetacentrics to form 2 small metacentrics. Since the geographic distribution is similar for both genera, and they live sympatrically, chromosomal rearrangements might have played a role in reproductive isolation in the course of their evolution from a *Xenotoca*-like ancestor. (*A. robustus* 3, 25/30 189618, 209823–24)

Allotoca Hubbs and Turner. 48stt, and 22M 2smst 2st. Fig. 2D, E.

As currently conceived, this genus contains two species. *A. dugesi* (Bean) is rather widely distributed in the Río Lerma basin and *A. maculata* Smith and Miller (1980), from Laguna Magdalena and vicinity, is very restricted.

Four populations (three of *A. dugesi*) were examined. *A. dugesi* has 26 chromosomes with 22 large metacentrics, but *A. maculata* has 48 subtelocentric-telocentrics, a complement probably representing the ancestral type. The two species are morphologically very similar though distinguishable on male coloration and pattern. They are allopatric and suggest that speciation has taken place in or near Laguna Magdalena and the form with 2n = 26 chromosomes, which was isolated from the laguna, has spread throughout the Río Lerma basin. This evolutionary change is designated karyotype orthoselection by White (1973:450). (*A. dugesi* 8, 209/

Fig. 2. Karyotypes of goodeid fishes. A = *Allodontichthys tamazulae*, 2n = 48, Río Terrero (M76-30), ♂; B = *Allodontichthys* sp., 2n = 48, Río de la Pola (M70-10) ♀; C = *Alloophorus robustus*, 2n = 30, Río Turbio (M76-22) ♀; D = *Allotoca dugesi*, 2n = 26, Presa El Jigante (M70-24) ♀; E = *Allotoca maculata*, 2n = 48, Laguna Magdalena (M70-12); F = *Ameca splendens*, 2n = 26, Río Teuchitlán (M66-17) ♀; G = *Ataeniobius toweri*, 2n = 48, La Media Luna (M68-18) ♂; H = *Chapalichthys encaustus*, 2n = 36, Río Tanhuato (M70-16) ♂; I = *Chapalichthys pardalis*, 2n = 36, El Agua de Zapote de Tocumbo (M71-9) ♀.

243, 189071, 189613, 189620; *A. maculata* 3, 53/56, 203851)

Ameca Miller and Fitzsimons. 22M 2m 2stt. Fig. 2F.

The monotypic genus *Ameca*, represented by *A. splendens*, is confined to the Río Ameca basin, Jalisco. The karyotype shows 26 chromosomes, including 22 large and 2 small metacentrics, and was probably derived from 48 subtelocentric-telocentrics through a fusion of 44 chromosomes to form 22 large metacentrics, and most likely a pericentric inversion in two chromosomes to form 2 small metacentrics. Morphologically and zoogeographically, *Ameca* seems close to *Xenotoca*, with 48 subtelocentric or telocentric chromosomes; the characters found in species of *Xenotoca* possibly represent the primitive condition. (*A. splendens* 6, 61/90, 209812)

Ataeniobius Hubbs and Turner. 2sm 46stt. Fig. 2G.

This monotypic genus is distributed in the upper Río Verde basin of the Río Pánuco drainage, which flows into the Gulf of Mexico (Fig. 1); it thus lives outside of the main distribution of the family. This fish (*A. toweri*) has been considered unique and primitive among goodeid fishes because of the lack of trophotaeniae in developing embryos (Hubbs and Turner, 1939). Karyotypic, morphologic and zoogeographic information, however, indicate that *Ataeniobius* is an advanced rather than a generalized goodeid and was probably derived from *Goodea*, which has a similar karyotype and is closely associated zoogeographically. It is thus hypothesized that *Ataeniobius* has lost its trophotaeniae secondarily. (*A. toweri* 2, 22/32, 209813)

Chapalichthys Meek. 12M 2sm 22stt. Fig. 2H, I.

Three species of this genus have been named but we recognize only two as valid at this time—*C. encaustus* (Jordan and Snyder) of the lower Río Lerma basin and *C. pardalis* Alvarez in a spring-fed upper tributary of the Río Balsas. Both appear to have the same karyotype. *C. peraticus* Alvarez, now possibly extinct, appears to be a synonym of *C. pardalis*. As discussed under *Alloophorus*, this genus might have shared the most recent common ancestor with *Alloophorus*. (*C. encaustus* 3, 49/53, 190841; *C. pardalis* 4, 42/44, 191685)

Characodon Günther. 24M. Fig. 3A.

Members of this monotypic genus live in Durango (and formerly in Coahuila), far to the north of the main range of other goodeids, and are readily distinguished from other goodeids (Miller and Fitzsimons, 1971; Fitzsimons, 1972). All of the chromosomes of *C. lateralis* Günther are large metacentrics, constituting the most derived karyotype in the family. This genus may have been derived from *Goodea*, *Xenotoca* or *Xenoophorus*, the latter being geographically closest to *Characodon* (Fig. 1). *Goodea* and *Xenoophorus* have a similar karyotype (2sm 46stt). (*C. lateralis* 2, 46/56, 209814)

Girardinichthys Bleeker. 48stt. Fig. 3B.

This genus has recently been regarded as comprising two species, *G. viviparus* (Bustamante), of the Valley of Mexico, and *G. multiradiatus* (Meek), of the upper Río Lerma basin (Miller and Fitzsimons, 1971). It has one of the primitive karyotypes and is morphologically close to the allopatric genus *Hubbsina*. Both apparently have the same karyotype, and both lack sensory pores on the preopercle, which is considered to be a derived trait and is the basis for considering them to be closely related. (*G. multiradiatus* 5, 114/126, 189604, 189605; *G. viviparus* 4, 27/32, 209817)

Goodea Jordan. 2sm 46stt. Fig. 3C.

This genus is easy to recognize by its compressed, large body with very posterior dorsal and anal fins, and the wide mouth and numerous gill rakers. It is the most widespread genus in the family. However, the number of species it contains has yet to be determined. We tentatively follow the conclusions of Hubbs and Turner (1939:Table I) that *Goodea* comprises three species: *G. atripinnis* Jordan, *G. gracilis* Hubbs and Turner and *G. luitpoldi* (Therese von Bayern and Steindachner). All three may also occur outside of the Río Lerma basin; *G. gracilis*, the northernmost, inhabits the Río Pánuco drainage on the Atlantic slope.

Six populations of these three species show similar karyotypes. As stated under *Ataeniobius*, *Goodea* (or a common progenitor) was probably

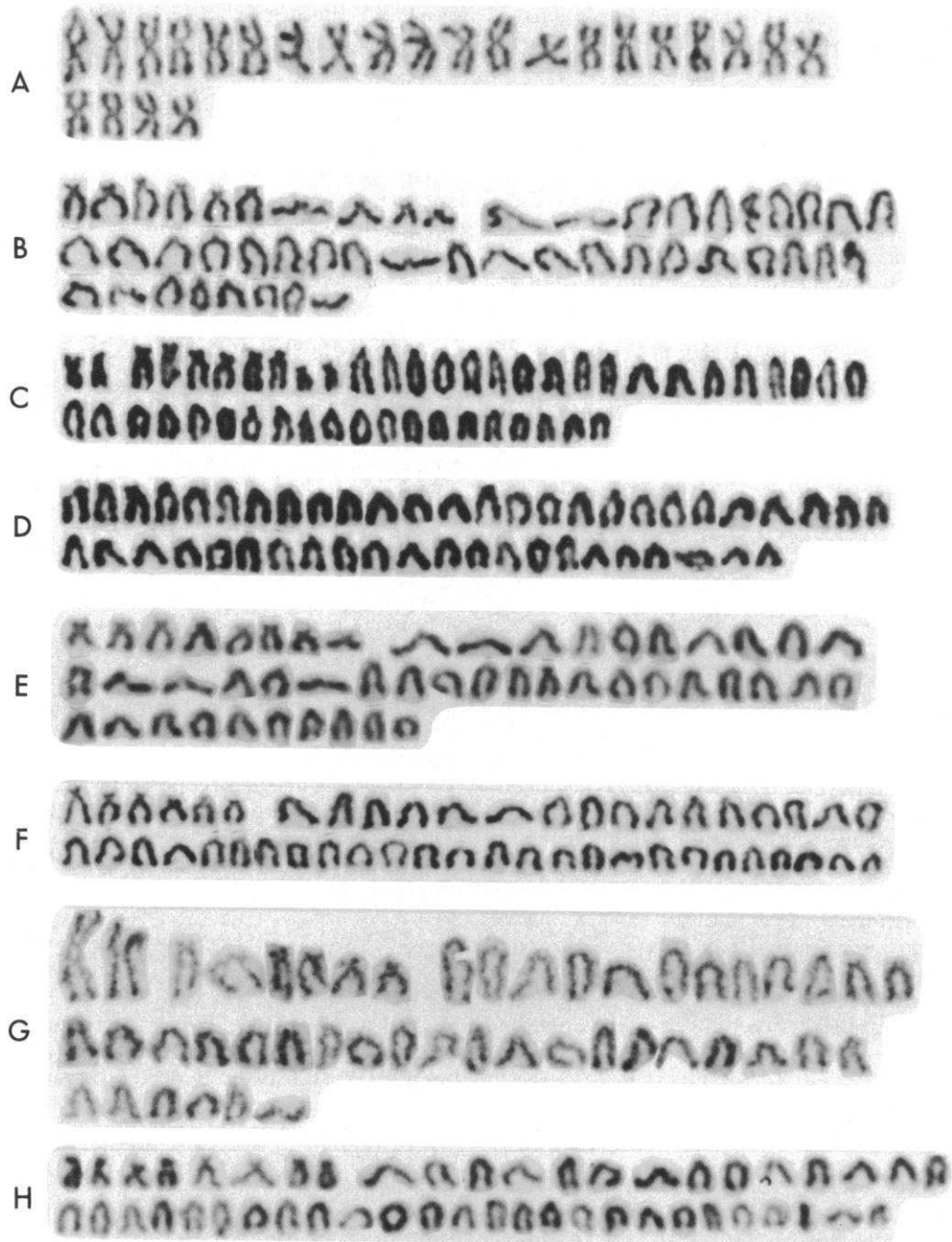

Fig. 3. Karyotypes of goodeid fishes. A = *Characodon lateralis*, 2n = 24, Los Berros (M68-41) ♀; B = *Girardinichthys multiradiatus*, 2n = 48, Río Lerma (M70-19) ♀; C = *Goodea gracilis*, 2n = 48, Río San Juan del Río (M76-25) ♂; D = *Hubbsina turneri*, 2n = 48, Canal de Queréndaro at Tzintzimeo (M71-11) ♀; E = *Ilyodon whitei*, 2n = 48, Río Nexapa (M66-12) ♂; F = *Neoophorus* sp., 2n = 48, Río Potrero Grande (M71-5) ♀; G = *Neoophorus meeki*, 2n = 46, Lago Zirahuén (M76-18) ♀; H = *Skiffia francesae*, 2n = 48, Río Teuchitlán (M70-11) ♀.

ancestral to *Ataeniobius*. *Xenoophorus* also has a similar karyotype. (*G. atripinnis* 1, 20/27, 189680; *G. gracilis* 2, 24/32, 189026, 198809; *G. luitpoldi* 1 ♀, 8/9, 189616)

Hubbsina de Buen. 48stt. Fig. 3D.

This monotypic genus, represented by *Hubbsina turneri* de Buen, is confined to the Río Grande de Morelia (interior) basin, and is considered to have the most recent common ancestor with *Girardinichthys*. Both of them have 48 subtelocentric-telocentric chromosomes, and lack sensory canal pores on the preopercular bones. (*H. turneri* 4, 35/42, 209815, 209819)

Ilyodon Eigenmann. 48stt, and various derived formulae. Fig. 3E.

This genus, recently expanded to include *Balsadichthys* (Miller and Fitzsimons, 1971), is also easily recognized by its large, fusiform body with a longitudinal dark band, but contains an undetermined number of valid species. At this time we recognize four: *I. furcidens* (Jordan and Gilbert), *I. whitei* (Meek), *I. xantusi* (Hubbs and Turner) and an undescribed species, all populations except one of which live south of the Mesa Central on the Pacific slope of Jalisco, Colima and Michoacán.

Karyotypes of 10 populations involving 7 phenotypes were examined. Six of these have primitive karyotypes with 48 subtelocentric-telocentrics, and the other forms were probably derived from one or some of these stocks. Populations of this genus in the Río Coahuayana basin indicate, by chromosomal and biochemical studies (Turner and Grosse, 1980), as well as by external morphology, that *Ilyodon* appears to be at a complex stage of speciation (see also Kingston, 1979). One population in Río Terrero shows polymorphism, with several different karyotypes: 4m 2sm 42stt, 2m 2sm 44stt and 3m 2sm 43stt. More exhaustive study of chromosomes is being undertaken and will be reported elsewhere. (*I. furcidens* 2, 34/40, 189075, 198845; *I. whitei* 5, 53/71, 189612, 189679; *I. xantusi* 1 ♀, 9/13, 189594; *I.* sp. 4, 54/73, 189586)

Neoophorus Hubbs and Turner. 2M 44stt. Fig. 3F, G.

We are uncertain about the number of valid species assignable to this genus. We definitely exclude *N. regalis* Alvarez (1959) which is clearly a valid species (we have examined the type series) but it is not clear to what genus it should be assigned, and was not available for karyotyping. We tentatively recognize three species, *N. diazi* (Meek), *N. meeki* Alvarez and *N. catarinae* de Buen, and for the present assign an undescribed species from the Río Ameca basin to this genus. Most of these fishes are restricted to isolated basins (L. Pátzcuaro, L. Zirahuén), formerly part of the Río Lerma system, and some headwater springs or spring-fed creeks of the Río Balsas basin. The karyotypes of all the isolated populations sampled are very similar (*N. catarinae* and *N. diazi* appear to be identical but *N. meeki* appears to have 6 rather than 4st chromosomes) and the consistent presence of 2 large metacentrics suggests a derived condition. The Río Ameca form differs, however, in lacking these two chromosomes and possibly represents the ancestral condition. (*N. catarinae* 2, 32/39, 189611; *N. diazi* 1, 14/17, 189615; *N. meeki* 1 ♀, 1/1—other data lost, 198815; *N.* sp. 2, 57/63, 191678)

Skiffia Meek. 22M 4stt, and various formulae. Figs. 3H, 4A–C.

This genus, which has a strong tendency for sexual dimorphism (male with a large dorsal fin, notched in 3 species, on a small body), was recently consolidated (Miller and Fitzsimons, 1971) and comprises three distinct lines: subgenus *Skiffia*, with *S. lermae* Meek; subgenus *Neotoca*, with *S. bilineata* (Bean); and subgenus *Ollentodon*, with *S. multipunctata* (Pellegrin) and *S. francesae* Kingston.

The karyotypes of all four species are distinct. *S. francesae* has 2n = 48 chromosomes, with 2 medium-sized metacentrics, and its closest (allopatric) relative, *S. multipunctata*, is polymorphic, with 2n = 44 or 46 chromosomes, including 2 to 4 large metacentrics of the Robertsonian type. *S. bilineata* has 2n = 48 chromosomes, without large metacentrics but with 4 medium-sized metacentrics, 2 submetacentrics, 34 subtelocentrics, and 8 acrocentrics. *S. lermae*, the type species of the genus, has 2n = 26 chromosomes, with 22 large metacentrics of the Robertsonian type plus 4 acrocentric chromosomes. (*S. bilineata* 2, 7/8, 209822; *S. francesae* 2, 11/11, 189588; *S. lermae* 2, 2/2—other data lost, 198812; *S. multipunctata* 4, 40/43, 209826)

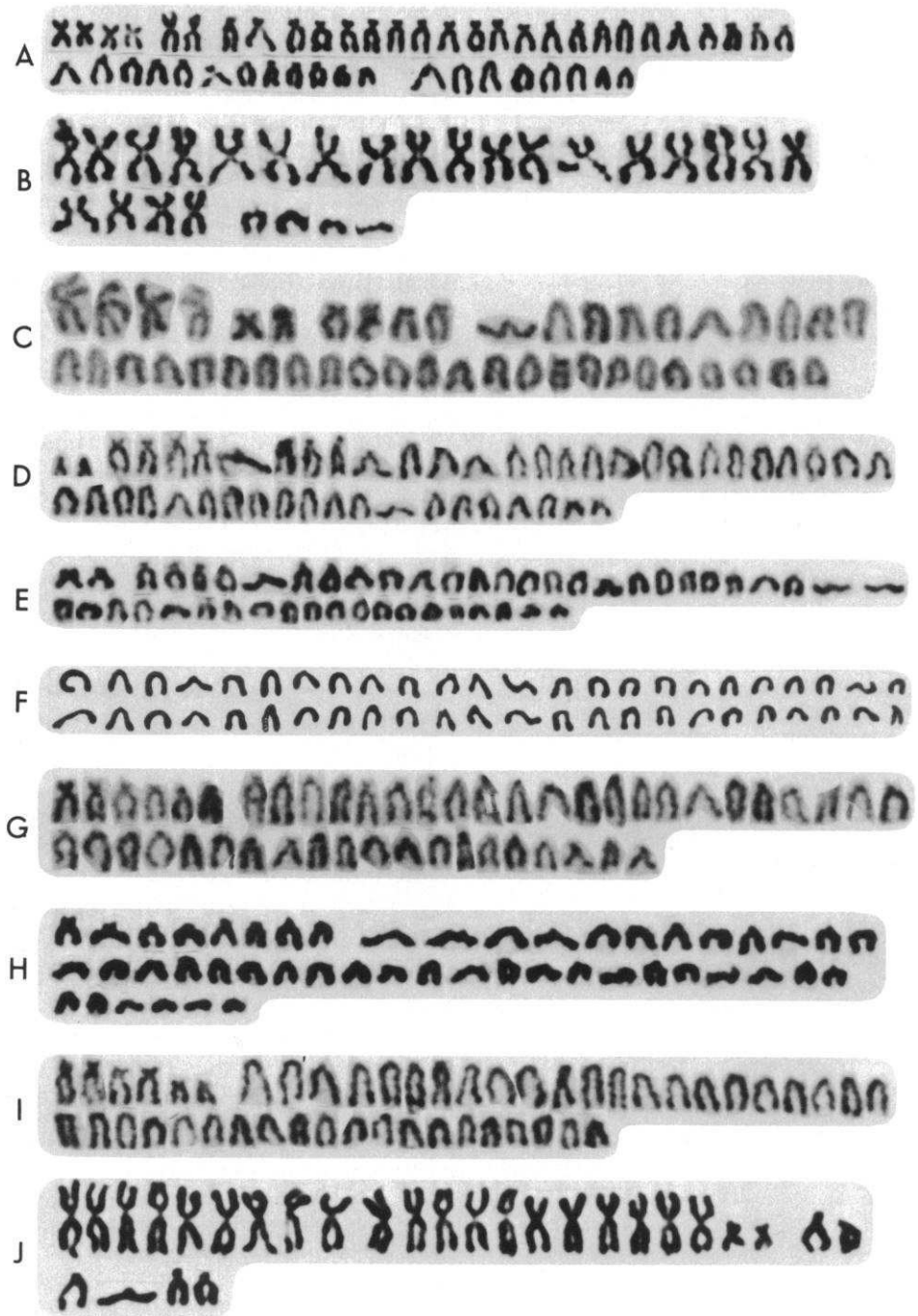

Fig. 4. Karyotypes of goodeid fishes. A = *Skiffia bilineata*, 2n = 48, canal at Tzintzimeo (M76-15) ♀; B = *Skiffia lermae*, 2n = 26, Rancho El Molino (M76-17) ♀; C = *Skiffia multipunctata*, 2n = 44, Lago de Camécuaro (M76-26) ♀; D = *Xenoophorus captivus*, 2n = 48, Río Santa María del Río (M66-8) ♂; E = *Xenoophorus captivus*, 2n = 48, Ojo de Agua de Moctezuma (M70-6) ♀; F = *Xenotaenia resolanae*, 2n = 48, tributary to Río Purificación (M66-15) ♀; G = *Xenotoca eiseni*, 2n = 48, Río San Leonel (M71-31) ♂; H = *Xenotoca melanosoma*, 2n = 48, Río Teuchitlán (M76-15) ♂; I = *Xenotoca variata*, 2n = 48, Lago de Cuitzeo (M70-27) ♂; J = *Zoogoneticus quitzeoensis*, 2n = 28, Ojo de Agua de Santiaguillo (M70-9) ♂.

Xenoophorus Hubbs and Turner. 2sm 46stt. Fig. 4D, E.

This genus is now regarded to be monotypic (Fitzsimons, 1979). Four populations, including the three nominal species recognized by Hubbs and Turner (1939), seem to have the same karyotype, although we did not obtain an analyzable spread for *X. erro*. This genus morphologically appears to be closely related to *Characodon* and perhaps is aligned with *Xenotoca* and its allies, but the karyotype shows more resemblance to *Goodea* as stated previously. (*X. captivus*, 209820)

Xenotaenia Turner. 48t. Fig. 4F.

This monotypic genus, with few bifid jaw teeth and distinctive trophotaeniae, is restricted to a few small Pacific-slope streams in southwestern Jalisco and western Colima, to the west of the Río Armería basin. Its distribution lies west of that of the genus *Allodontichthys*. The karyotype of *Xenotaenia* differs from that of *Allodontichthys* in lacking the pair of small metacentrics and the pair of submetacentrics and hence is more primitive. (*X. resolanae* 2, 20/30, 186293)

Xenotoca Hubbs and Turner. 48stt. Fig. 4G–I.

Fitzsimons (1972) analyzed the species in this genus, which comprises *X. eiseni* (Rutter), *X. melanosoma* Fitzsimons and *X. variata* (Bean). Each has a distinctive karyotype. *Xenotoca* may be ancestral to *Ameca* and *Xenoophorus*. (*X. eiseni* 5, 36/50, 172243, 186290; *X. melanosoma* 5, 20/28, 186292, 192123; *X. variata* 5, 65/86, 189025, 189073)

Zoogoneticus Meek. 20M 2m 6stt. Fig. 4J.

We recognize *Zoogoneticus quitzeoensis* (Bean) as a monotypic genus with only 28 chromosomes, of which 20 are large metacentrics. Its closest relative is not yet apparent. (*Z. quitzeoensis* 5, 75/80, 189582)

Considerations and Conclusions

Significance and limitations of karyologic data.—Although there have been many studies on fish chromosomes, few of these have dealt with an entire group (tribe, subfamily or family) for which the geologic history of the distributional range and the morphologic features are well known, as in the Goodeidae. Such information is important in order to understand or evaluate the systematic significance of chromosomal variations. We have previously demonstrated that, in the middle Colorado River plagopterine minnows, karyotypic changes proceeded in the same direction as morphologic changes (Uyeno and Miller, 1973).

Species with the most generalized and least modified karyotypes were chosen from each genus for comparison, since derived forms often exhibit secondary changes that obscure generic relationships (Table 1). In the Goodeidae (as in many other fishes—Denton, 1973:147), a diploid set of 48 acrocentrics is considered to be the ancestral karyotype. The diploid number that recurs consistently in other cyprinodontiforms (many Cyprinodontidae, including all known forms of *Cyprinodon*) is also 48. For example, 2n = 48 occurs in both *Empetrichthys* and *Crenichthys*, regarded by Parenti (1981) as the closest relatives of the Goodeidae. Our examination shows that *Profundulus* and *Rivulus* also have a diploid chromosome number of 48. This is also the most prevalent diploid number among other cyprinodontoids. In attempting to determine relationships from karyotypes, large metacentrics resulting from Robertsonian fusion were considered as two acrocentrics because centromeric fusion seems to have occurred readily within a genus or among very closely related species and may not always indicate strong divergence.

Two interrelationships, suggested here for the first time, are indicated from karyotypic data. First, rather than regarding *Ataeniobius* as the most primitive goodeid genus (as held by Hubbs and Turner, 1939), we view it as a possible derivative of *Goodea* or at least from a group ancestral to both of these genera. Second, *Allodontichthys hubbsi*, with multiple sex chromosomes (Uyeno and Miller, 1972; Miller and Uyeno, 1980), is regarded to be descended from *A. tamazulae*.

Taxonomic implications.—Although four reports (Mendoza, 1956, 1965; Miller and Fitzsimons, 1971; Fitzsimons, 1972) published since the 1939 family revision indicate that anatomical features of the trophotaeniae and ovary used by Hubbs and Turner are too variable in certain species to be used alone as a basis for family classification, the study by Miller and Fitzsimons (1971) is the only one that appreciably altered their classification. These authors placed four genera and one species from the Hubbs-Turner scheme into synonymy and suggested that the

designation of subfamilies and phyletic lines requires further study to determine if these categories actually reflect a natural classification. These synonymies and suggestions are evaluated in the light of karyotypic data provided for the first time in this report.

The genus *Ataeniobius,* which was probably derived from *Goodea,* has, like that genus, 2 submetacentrics and 46 acrocentric-subtelocentrics. *Allodontichthys hubbsi,* with multiple sex chromosomes, is morphologically and zoogeographically derivable from *A. tamazulae,* which has a similar karyotype, 2m 2sm 44stt.

Miller and Fitzsimons (1971) agreed with the suggestion by Hubbs and Turner (1939) that *Balsadichthys* is closely related to *Ilyodon* and might eventually be regarded as a junior synonym. Cytological data confirm the basis for the generic synonymy: the two species (*I. whitei* and *I. xantusi*) formerly included in *Balsadichthys* have a karyotype identical to that of the species (*I. furcidens*) included in *Ilyodon* by Hubbs and Turner (1939:Table I). The basis for the inclusion of *Lermichthys* in *Girardinichthys* is supported by the identical karyotypes of *G. multiradiatus,* formerly in *Lermichthys,* and *G. viviparus* [This species was formerly called *G. innominatus* but that name is preoccupied by *G. viviparus* (Alvarez and Navarro, 1957)]. Miller and Fitzsimons proposed that the monotypic genera *Ollentodon* and *Neotoca* be synonymized with the older name *Skiffia* and that the two species of *Skiffia, S. lermae* and *S. variegata,* be regarded as a single entity, *S. lermae.* Polymorphism, recently detected in *Skiffia,* is not yet fully understood. The alliance of *Skiffia multipunctata* (formerly *Ollentodon*), *S. bilineata* (formerly *Neotoca*) and *S. francesae* (Kingston, 1978) from the Río Teuchitlán is suggested by their similarity in chromosome number and centromere attachments, although *S. bilineata* is distinguished from the other two in certain morphological and color features. However, the affinity of these species with *Skiffia lermae* (2n = 26) is not reflected in the gross structure of the chromosome complements. Cytological data available on the "*Skiffia* complex" are primarily heuristic: they do not solve a problem but point to it. Further study is now underway to combine karyology with a variety of other information sources to elucidate relationships within the species now included in *Skiffia.*

Except for the monotypic Characodontinae, each subfamily in the Hubbs-Turner classification contains one or more genera whose species exhibit the ancestral diploid chromosome number of 48. Similarly, eight of the family's 11 phyletic lines include at least one genus whose members have 48 chromosomes in the diploid complement. Derivations from the ancestral character state via reduction in chromosome number occur in the two subfamilies that are not monotypic, the Goodeinae and Girardinichthyinae. Within the Goodeinae alone, reduction occurs in four of six phyletic lines. Interpretation of cytological data in strict accordance with the Hubbs-Turner classification forces the conclusion that the evolution of karyotypes in a similar fashion from primitive to derived character states has occurred independently in five phyletic lines representing two subfamilies. The likelihood of such a high degree of convergence may be questioned. The elaboration of a satisfactory natural classification of the family based on several sources of information must wait until species limits and interrelationships of these interesting fishes are more clearly understood.

When describing *Hubbsina turneri,* de Buen (1941) assigned this monotypic genus to the Goodeinae on the basis of ovarian features specified for the subfamily by Hubbs and Turner. Mendoza (1956) agreed that the structure of the ovary of *H. turneri* is the same as that outlined for the Goodeinae but noted that the trophotaeniae, which were not examined by de Buen, conform to the Hubbs-Turner description for two other subfamilies, the Characodontinae and the Girardinichthyinae. Combining the findings of Mendoza's study with information concerning median fins, gill rakers and the cephalic sensory system, Miller and Fitzsimons (1971) argued that *H. turneri* should be removed from the Goodeinae and placed in the Girardinichthyinae close to *Girardinichthys.* Chromosome data are compatible with the argument aligning *Hubbsina* with *Girardinichthys* (Table 1). The karyotype of the monotypic *Hubbsina* contains only subtelocentrics and telocentrics, as in the species of *Girardinichthys,* and lacks the pair of submetacentrics characteristic of *Goodea.*

Comparison of the karyotypic information in Table 1 with the classification by Hubbs and Turner (1939:Table II), which is based on ovarian characters and the nature of the trophotaeniae, shows that: 1) Recognition of Ataeniobinae is not justified, especially if lack of trophotaeniae is a primitive character (as Hubbs and Turner believed); the chromosome data in-

dicate that *Ataeniobius* is closely related to *Goodea* (to which genus the type species was initially referred). Lack of trophotaeniae may represent a secondary loss. 2) Other subfamily alignments by Hubbs and Turner are discordant with the chromosome data.

Study of Table 1 leads us to make the following provisional groupings of genera that seem to represent species more closely related to each other than to other such segregated groups. Study of the cephalic lateralis system (Fitzsimons, 1981) supports these tentative groupings.

1) *Goodea* and *Ataeniobius*, for reasons mentioned above and also their seemingly identical karyotypes.

2) *Chapalichthys, Xenotoca, Ameca* and perhaps *Alloophorus*. All of these have a high number (8–10) of preopercular pores and the ovarian septum entire and attached to the ovary dorsally and ventrally. Karyotypes are variable, however.

3) *Allotoca* and *Neoophorus*. The species in these genera lack pores 4b to 6 on top of the head, have mostly 10 preopercular pores, and the ovarian septum is divided (whether *Xenoophorus* belongs here is unclear). Most of the species have a diploid number of 46 or 48 chromosomes, a large number of which are telocentric.

4) *Skiffia, Girardinichthys* and *Hubbsina*. In these the supraorbital canal (and most of the other canal systems) is entirely replaced by pit organs. Except for *Skiffia lermae*, all species in these genera have 2n = 48 or 46 and 38 to 40 acrocentric chromosomes.

It is clear from repeated alterations in karyotype number and structure within what seem to be natural lines, that there has been considerable homoplasy among the karyotypes of these groups.

In spite of the above useful information based on karyotypes, it is impossible to delineate relationships totally on the basis of karyotypes. A single character, such as the trophotaeniae or karyotype, does not enable one to distinguish parallel from ancestral-descendent changes. For example, Robertsonian fusions, pericentric inversions or other changes that alter the forms of chromosomes can take place independently in various groups. However, karyotypes are conservative enough to reveal the closeness of some taxa, as shown by the common possession in all species of the genus *Goodea* of a pair of submetacentric chromosomes; such a pair is also characteristic of the monotypic genus *Ataeniobius* which suggests an intimate relationship between these two genera. When one finds karyotypic data to be significantly different between groups thought to be closely related on the basis of conventional morphology, a reexamination of the relationship is indicated; this was done with *Hubbsina turneri*, as explained above.

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